JNeurosci Accepted Manuscript

Research Report: Regular Manuscript

Distinct oscillatory dynamics underlie different components of hierarchical cognitive control

1   **Title**

2   Distinct oscillatory dynamics underlie different components of hierarchical cognitive control

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24   **Number of pages:** 30

25   **Number of figures:** 8

26   **Number of words:** Abstract – 225; Introduction – 517; Discussion – 1511

27   **Conflicts of Interest**

28   The authors declare no competing financial interests.

29   **Acknowledgements**

35   **Abstract**

36

37   Hierarchical cognitive control enables us to execute actions guided by abstract goals. Previous

38   research has suggested that neuronal oscillations at different frequency bands are associated

39   with top-down cognitive control, however, whether distinct neural oscillations have similar or

40   different functions for cognitive control is not well understood. The aim of the current study was

41   to investigate the oscillatory neuronal mechanisms underlying two distinct components of

42   hierarchical cognitive control: the level of abstraction of a rule, and the number of rules that

43   must be maintained (set-size). We collected electroencephalography (EEG) data in 31 men and

44   women who performed a hierarchical cognitive control task that varied in levels of abstraction

45   and set-size. Results from time-frequency analysis in frontal electrodes showed an increase in

46   theta amplitude for increased set-size, whereas an increase in delta was associated with

47   increased abstraction. Both theta and delta amplitude correlated with behavioral performance in

48   the tasks but in an opposite manner: theta correlated with response time slowing when the

49   number of rules increased whereas delta correlated with response time when rules became

50   more abstract. Phase amplitude coupling analysis revealed that delta phase coupled with beta

51   amplitude during conditions with a higher level of abstraction, whereby beta band may

52   potentially represent motor output that was guided by the delta phase. These results suggest

53   that distinct neural oscillatory mechanisms underlie different components of hierarchical

54   cognitive control.

55   **Significance Statement**

56

57   Cognitive control allows us to perform immediate actions while maintaining more abstract,

58   overarching goals in mind and to choose between competing actions. We found distinct

59   oscillatory signatures that correspond to two different components of hierarchical control: the

60   level of abstraction of a rule and the number of rules in competition. An increase in the level of

61   abstraction was associated with delta oscillations, whereas theta oscillations were observed

62   when the number of rules increased. Oscillatory amplitude correlated with behavioral

63   performance in the task. Finally, the expression of beta amplitude was coordinated via the

64   phase of delta oscillations, and theta phase coupled with gamma amplitude. These results

65   suggest that distinct neural oscillatory mechanisms underlie different components of hierarchical

66   cognitive control.

67   **Introduction**

68

69   Cognitive control orchestrates thoughts and actions according to internal goals (Norman and

70   Shallice 1986, Braver 2012). The frontal cortex is central to cognitive control, where

71   representations of rules and goals provide top-down influences over motor and perceptual

72   systems to guide actions (Miller and Cohen 2001, Miller and D'Esposito 2005, Badre and Nee

73   2018, Vogelsang and D'Esposito 2018). Previous research findings suggest that the frontal

74   cortex is organized hierarchically along the rostral-caudal axis, where the caudal frontal cortex is

75   involved in the control of concrete action representations, whereas the rostral prefrontal cortex

76   is involved in the control of abstract rules, goals, and contexts (Badre and Nee 2018). We have

77   previously demonstrated that at any particular level of representation, an appropriate action can

78   be chosen from a number of competing rules (number of rules defined as set-size), and as

79   competition increases, cognitive control is required to adjudicate among alternatives (Badre and

80   D'Esposito 2007).

81   It is proposed that rhythmic neural oscillations support a diverse range of cognitive

82   functions, whereby oscillations in different frequency bands, ranging from slow delta oscillations

83   to faster gamma oscillations, are generated by distinct biophysical mechanisms and are

84   associated with different cognitive functions (for reviews see: (Sauseng, Griesmayr et al. 2010,

85   Roux and Uhlhaas 2014, Helfrich and Knight 2016, Sadaghiani and Kleinschmidt 2016, Helfrich,

86   Breska et al. 2019)). Phase amplitude coupling (PAC) between frequency bands, in which the

87   phase of a slow oscillation like theta can modulate the amplitude of faster oscillations like

88   gamma (Lisman and Jensen 2013, Nácher, Ledberg et al. 2013, Arnal, Doelling et al. 2014,

89   Morillas-Romero, Tortella-Feliu et al. 2015, Voytek, Kayser et al. 2015, Heusser, Poeppel et al.

90   2016), further supports inter-areal communication and interactions between cognitive functions.

91   However, whether or not there are distinct neural oscillations associated with different

92   components of hierarchical cognitive control is unknown.

93   In our previous human electrocorticography (ECoG) study, we found that tasks that

94   required increased hierarchical cognitive control were associated with increased theta-band

95   synchronization between the prefrontal and premotor/motor regions (Voytek, Kayser et al.

96   2015). Furthermore, the phase of prefrontal theta oscillations showed increased coupling with

97   the amplitude of gamma oscillations in the motor cortex (Voytek, Kayser et al. 2015). A series of

98   non-human primate experiments have also found that beta-band oscillations are associated with

99   rule representation in the frontal cortex, in which distinct neural populations represent different

100   rules, and become more synchronized in beta frequency when the rule is behaviorally relevant

101   (Buschman, Denovellis et al. 2012, Antzoulatos and Miller 2014, Antzoulatos and Miller 2016,

102   Wutz, Loonis et al. 2018). Furthermore, updating the active rule representation increases delta

103   oscillations in these same neural populations, preceded by a modulation in beta oscillations

104   (Antzoulatos and Miller 2016). Together, these findings suggest that theta-gamma and delta-

105   beta band oscillations are associated with hierarchical cognitive control. However, in these

106   experiments, tasks that engaged more abstract rules also had higher set-size (higher number of

107   rules to select from), making it impossible to determine if the modulation of neural oscillations

108   and phase-amplitude coupling by these cognitive processes are driven by set size or

109   abstraction. In this study, our aim was to address this question.

110

111   **Materials and Methods**

112

113   *Experimental Design and Statistical Analysis*

114   Thirty-one healthy participants (18 females; mean age = 20 years; range 18-34) with

115   normal or corrected to normal vision were recruited from the University of California, Berkeley.

116   Written consent was obtained prior to the start of the experiment and participants received

117   monetary compensation for their participation. The study was approved by the University of

118   California, Berkeley Committee for Protection of Human Subjects.

119   The experiment consisted of a single session of EEG during performance of the

120   hierarchical cognitive control task. Behavioral performance, response time and accuracy, was

121   analyzed using two-way repeated-measures ANOVA with two factors: abstraction (high and low)

122   and set-size (high and low). Time frequency analysis was conducted using stimulus and

123   response-locked epochs for the abstraction and set-size contrast. The time frequency analysis

124   was restricted to a midfrontal electrode cluster that was defined using hierarchical clustering of

125   the time frequency data independent of the contrasts of interest. We corrected for multiple

126   comparisons and spurious findings using permutation testing with significance determined by

127   cluster mass across all seven electrode clusters for the abstraction and set-size contrast. Next,

128   the significant time frequency bands were correlated with response time as a function of

129   abstraction and set-size using Pearson correlation. Finally, phase amplitude coupling (PAC)

130   was computed between delta phase and beta amplitude and theta phase and gamma amplitude

131   for each task condition. PAC values were inputted to a two-way repeated-measures ANOVA

132   with two factors: abstraction and set-size.

133

134   *Experimental Task*

135   The task used in this study was adapted from two previously published studies (Badre

136   and D'Esposito 2007, Badre and D'esposito 2009, Voytek, Kayser et al. 2015). We manipulated

137   two components of hierarchical cognitive control, abstraction and set-size (see Figure 1A).

138   During the response task (low abstraction conditions), participants learned the association

139   between a colored square and a button response. The response task had two levels of set-size:

140   a low set-size condition (in which four colored squares had to be associated with four

141   responses) and a high set-size condition (in which eight different colored squares had to be

142   associated with eight response options; Figure 1A). In the dimension task (high abstract

143   conditions), participants were presented with a colored square that contained two objects. The

144   color of the square indicated the dimension (shape or texture) by which the participant had to

145   evaluate the two objects. Importantly, the abstraction task contained two levels of set-size

146   similar to the response task: a low level of set-size and yet still higher in abstraction and a

147   higher level of set-size and also high in abstraction (see Figure 1A). In the high abstraction, low

148   set-size condition, participants made a judgement along only one dimension (either shape or

149   texture) as both colored squares mapped to a single dimension (e.g. a purple square or a green

150   square signal that participants must judge whether the two objects have the same or different

151   shape). In the high abstraction, high set-size condition, two colored squares mapped to two

152   different dimensions (e.g. the color red indicates a perceptual judgement along the shape

153   dimension, the color blue indicates the texture dimension).

154   Our previous versions of the experiment (Badre and D'Esposito 2007, Voytek, Kayser et

155   al. 2015) did not match performance between the low and high abstraction tasks, as the highest

156   set-size condition of a low abstraction task showed worse performance than the lowest set-size

157   of a high abstraction task. By matching performance across levels of abstraction, we remove a

158   potential confound of task difficulty in isolating the processing of abstract rule representations

159   (Todd, Nystrom et al. 2013). To match performance between levels of abstraction, we ran

160   multiple pilot experiments, in which we increased the difficulty of the response task into a

161   comparable performance range as the dimensions task. In particular, we iteratively increased

162   the number of competing rules in the response task and shorted the response window from

163   three to two seconds to increase response time and reduce the accuracy of participants for the

164   response task. At the completion of this pilot testing, we selected two conditions to be defined

165   as low set-size based on performance levels: the response task with four responses and the

166   dimensions task with one dimension. For the high set-size conditions, we used the response

167   task with eight responses and the dimension task with two dimensions.

168   In the experiment, participants performed eight blocks, two of each of the four

169   conditions. Each block contained 48 trials; thus, each participant completed 96 trials per

170   experimental condition. Each trial was presented on the screen for two seconds and participants

171   were instructed to provide their response within that time window. Each trial was separated by a

172   fixation cross that varied exponentially in length from three to ten seconds. The experiment was

173   programmed in Psychtoolbox implemented in MatLab 2015a (The MathWorks, Inc.). Prior to the

174   start of the experimental task, participants were instructed to maintain their gaze on a fixation

175   point and to remain still for five minutes with eyes open followed by five minutes eyes closed.

176   This resting-state EEG data was not analyzed for the purpose of this paper.

177

178   *EEG Recording and Preprocessing*

179   EEG data was recorded from 64 active electrodes using a BioSemi ActiveTwo amplifier

180   with Ag-AgCl pin-type active electrodes mounted on an elastic cap according to the extended

181   10-20 system (BioSemi, Amsterdam, Netherlands). In addition, four electrodes were used to

182   monitor horizontal and vertical eye movements and two electrodes recorded electrical activity

183   from the mastoids. Signals were amplified and digitized at 1,024 Hz and stored for offline

184   analysis. Participants were trained before the experiment to minimize eye movements, blinking,

185   and muscle movement before the experiment.

186   The EEG data were analyzed with the software package EEGLab14 (Delorme and

187   Makeig, 2004) which utilized MatLab2015a (The MathWorks, Inc.). The continuous EEG data

188   were re-referenced to an average of the mastoid electrodes and filtered digitally with a

189   bandpass of 0.1-100Hz (two-way least-squares finite impulse response filter). The continuous

190   data were then divided into epochs ranging from −1000 milliseconds before stimulus onset until

191   2000 milliseconds post-stimulus onset. The epochs in the EEG data were visually inspected and

192   trials that contained excessive noise, such as muscle artifacts, were removed, resulting in an

193   average of 4.5% of trials that were removed across participants. Furthermore, electrode

194   channels with excessive noise were identified by visual inspection and reconstructed using the

195   average of neighboring electrodes. Eye-blinks and other EEG related artifacts were identified

196 and rejected using the extended info-max independent component analysis using the EEGLab

197 toolbox with default mode training parameters (Delorme and Makeig 2004).

198

199 *Electrode clustering*

200   Electrode clusters were defined based on a data-driven hierarchical clustering approach

201 that grouped electrodes based on the similarity of the evoked oscillatory amplitude that ranged

202 from 2-30Hz (see for similar procedure (Clarke, Roberts et al. 2018). Time-frequency

203 decomposition was averaged across all trials, conditions, and participants. Data from each

204 electrode was vectorized such that it included all time points and frequencies. A distance metric

205 was calculated for each electrode based on the similarity in evoked spectral response. An

206 agglomerative hierarchical clustering algorithm was applied that grouped pairs of electrodes

207 with the most similar spectral response. The two most similar electrode pairs were averaged.

208 This process continued until all electrodes were paired under a single tree. A dendrogram of the

209 hierarchical clusters was created and only clusters that fit an a priori cluster scheme based on

210 Clarke et al. (2018) were included in the time-frequency analysis. Each electrode cluster was

211 defined to only included contiguous electrodes and we excluded electrode clusters with less

212 than three electrodes. This hierarchical clustering approach resulted in six electrode clusters

213 that were used in the main analysis (Figure 2). Results reported here for an electrode cluster is

214 the averaged spectral response of all electrodes within the cluster. Our previous evidence using

215 this task in fMRI (Badre and D'Esposito 2007) and electrocorticography (Voytek, Kayser et al.

216 2015) found task-modulated activity related to cognitive control in lateral prefrontal cortex.

217 However, due to the problem of volume conduction and electric field properties in EEG,

218 activation of bilateral sites is commonly found in the midline (Sasaki, Tsujimoto et al. 1996,

219 Stropahl, Bauer et al. 2018, Riddle, Ahn et al. 2020). Therefore, we focused our analysis on the

220 frontal midline electrode cluster and capitalized on the temporal resolution afforded by EEG. We

221   hypothesized that the frontal midline electrode clusters (highlighted in Figure 2) would show the

222   strongest effects of hierarchical cognitive control (see (Cavanagh and Frank 2014) for review).

223

224   *Time-frequency Analysis*

225   Time-frequency analysis was applied using six cycle Morlet wavelet in the frequency

226   range of 2 to 50 Hz with steps of 1 Hz between each wavelet center. The Morlet wavelets were

227   applied to sliding time windows of 20 milliseconds increments in the entire epoch ranging from -

228   1000 milliseconds to 2000 milliseconds with stimulus onset set as time 0. To minimize the

229   problem of edge artifacts, we concatenated mirrored (i.e. time inverted) segments before and

230   after the task epoch (Cohen 2014). Time-frequency analysis was performed on these extended

231   epochs and mirrored segments were discarded from the final analysis (see for similar procedure

232   (Fell and Axmacher 2011, Vogelsang, Gruber et al. 2018). Results reported here were not

233   baseline corrected since we were interested in differences across conditions and therefore

234   baseline correction is not necessary (see for similar approaches (Fell and Axmacher 2011,

235   Gruber, Watrous et al. 2013, Vogelsang, Gruber et al. 2018)). For each of the four experimental

236   conditions, only trials in which the participant made a correct response were included in the

237   analysis. Trial numbers used in the analysis were: low abstraction, low set-size mean(std) =

238   92.4(4.8), range 76 - 96; low abstraction, high set-size mean(std) = 88.1(8.0), range 56-96; high

239   abstraction, low set-size mean(std) = 91.8(6.8), range 68-96; high abstraction, high set-size

240   mean(std) = 87.1(7.4), range 68-96. Our main analysis was two contrasts, one for "abstraction"

241   (high versus low) and one for "set-size" (high versus low).

242   An across participant non-parametric statistical approach was applied to test for

243   significant time-frequency differences between the contrasts of interest. We ran cluster-mass

244   permutation testing in which the average t-value within a significant cluster ($p < 0.05$) is used to

245   evaluate significance. The permutation testing procedure consisted of the following steps. First,

246   we computed the cluster mass for each of the contrasts of interest (abstraction and set-size) for

247   each of the six electrode clusters. Second, the experimental conditions for the abstraction (or

248   set-size) contrast were randomly swapped for 50% of the participants such that any systematic

249   differences between the conditions were eliminated. We ran the contrast for this randomized

250   pairing and calculated the largest absolute cluster mass across all electrode clusters. This

251   randomization process was repeated 1000 times to create a null distribution of the largest

252   negative and positive cluster mass values. Using an alpha level of .05 with 1000 permutations,

253   we used the 25th and 975th values to represent the critical mass values, and values below or

254   higher than these values were considered to be significant effects. This stringent procedure

255   allowed us to control for multiple comparisons across the electrode clusters (Blair and Karniski

256   1993, Maris and Oostenveld 2007).

257

258   *Phase Amplitude Coupling Analysis*

259   In addition to a time-frequency analysis, we also sought evidence for how different

260   frequency bands may interact with each other during hierarchical cognitive control. One possible

261   mechanism is phase amplitude coupling (PAC), which involves examining the relationship

262   between the phase of a lower frequency band (e.g. delta and theta) and the amplitude of a

263   higher frequency band (e.g. beta and gamma). To examine whether the phase of slow

264   oscillatory bands modulated the amplitude of faster frequency bands as a function of increased

265   rule abstraction and rule set-size, we computed PAC for the phase of slow frequency bands in

266   the range of 2-7 Hz, which includes delta and theta, with the amplitude of the higher frequency

267   spectrum ranging from 10-49 Hz separately for each task condition. We narrowed our analysis

268   to the coupled pairs motivated by our time-frequency analysis and a priori based on our

269   previous findings (Voytek, Kayser et al. 2015).

270   To compute PAC, we extracted the phase of the delta and theta frequency bands using

271   a three cycle Morlet wavelet convolution and the amplitude of the higher frequencies using a

272   five cycle Morlet wavelet convolution. We selected these parameters such that the half width full

273 mass of the low and high frequencies were more closely matched (Cohen 2019). We calculated

274 PAC using the phase and amplitude values from the significant time windows observed in the

275 time-frequency contrast for delta band (200 to 1400 milliseconds) and theta band (600 to 1200

276 milliseconds). For each participant, the phase (θ) and amplitude (M) values of each trial were

277 concatenated into a single continuous time series (n is the number of time points) and PAC was

278 calculated according to **Formula 1**.

279 $$\textbf{Formula 1}.\ PAC = \left|\frac{\sum_{t=1}^{n} M * e^{i\theta}}{n}\right|$$

280 We applied nonparametric permutation testing to determine whether the obtained PAC

281 values would be expected given the null hypothesis of no relationship between phase and

282 amplitude. The permutation procedure involved temporally shifting the amplitude values with a

283 random temporal offset of at least 10% the length of the time series and calculating PAC

284 (Cohen 2014). After 1000 repetitions, PAC is converted into a z-score from the null distribution,

285 resulting in PAC_z. We were interested in changes in PAC_z with increased abstraction and set-

286 size. In order to reduce multiple comparisons, we used a priori coupled pairs for the

287 hypothesized coupled frequencies based on the time-frequency analysis and ran a two-way

288 repeated-measures ANOVA of within-participant factors: abstraction and set-size.

289

290 *Code and Data Availability*

291 Custom code used for these analyses are available upon request to the corresponding

292 author. The authors assert that all requests for raw data within reason will be fulfilled by the

293 corresponding author.

294

295 **Results**

296

297 *Behavioral Results*

298   The task was designed to separately manipulate abstraction and set size during

299 hierarchical cognitive control. To test the effects of our behavioral manipulation, we performed

300 separate two-way repeated-measures ANOVA. We entered two independent variables:

301 abstraction (low, high) and set-size (low, high), and response time (RT) and accuracy as

302 dependent variables. For RT, the ANOVA revealed a significant main effect of abstraction (high

303 abstraction mean = 1132.0, sd = 105.3 milliseconds; low abstraction mean = 974.1, sd = 95.0

304 milliseconds; $F(1,30) = 398$, $p < 0.0001$, $\eta^2_p = 0.93$), a main effect of set-size (high set-size mean

305 = 1176.0, sd = 95.7 milliseconds; low set-size mean = 930.1, sd = 95.5 milliseconds; $F(1,30) =$

306 92.1, $p < 0.0001$, $\eta^2_p = 0.75$), and an interaction ($F(1,30) = 53.1$, $p < 0.0001$, $\eta^2_p = 0.64$) (Figure

307 1B). Participants were slower as a function of abstraction and set-size. For accuracy, the

308 ANOVA revealed a main effect of set-size (high set-size mean = 94.7%, sd = 5.0%; low set-size

309 mean = 97.7%, sd = 2.9%; $F(1,30) = 10.2$, $p = 0.003$, $\eta^2_p = 0.25$), but did not reveal a significant

310 main effect of abstraction ($F(1,30) = 0.11$, $p = 0.75$, $\eta^2_p = 0.0036$) or interaction (Figure 1C).

311 Participants were less accurate for the conditions that required maintenance of a larger set-size,

312 but behavior was matched across levels of abstraction.

313

314 *Time-Frequency Results*

315   We performed time-frequency analyses to determine how set-size and abstraction

316 modulates patterns of neural oscillations during hierarchical cognitive control. The time-

317 frequency analyses focused on the spectral amplitude differences ranging from 2 to 50 Hz in the

318 entire epoch time window (-1000 to 2000 milliseconds relative to stimulus onset) for both the

319 abstraction and set-size contrast (high versus low abstraction and high versus low set size). For

320 the abstraction contrast (Figure 3A), across all electrode clusters, there was a significant

321 increase in the delta frequency band (2-3 Hz) from 100 to 2000 milliseconds post stimulus onset

322 and a significant decrease in the beta frequency band (peak at 12-22 Hz) from 500 to 1500

323 milliseconds post stimulus onset (peak at 500 to 1000 milliseconds) for all electrode clusters. In

324   the topographic plots, it can be seen that in the abstraction contrast, delta amplitude showed the

325   strongest increase in mid and right frontal electrode clusters (Figure 3B) whereas beta

326   amplitude showed the strongest decrease in the mid frontal electrode cluster (Figure 3C). For

327   the set-size contrast (Figure 3D), across all electrode clusters, there was a significant increase

328   in amplitude in the theta frequency band (4-6 Hz) from 850 to 1700 milliseconds post stimulus

329   onset. There was a significant decrease in amplitude in the beta frequency band (12-30 Hz)

330   around 500 to 1500 milliseconds after stimulus onset in frontal midline electrode cluster, and

331   500 to 1800 milliseconds after stimulus onset in central and posterior electrode clusters. In the

332   topographic plots, it can be seen that in the set-size contrast, theta amplitude showed the

333   strongest increase in the frontal midline electrode cluster and beta amplitude showed the

334   strongest decrease in the frontal midline and central midline electrode clusters. Altogether, two

335   different low frequency bands increased in amplitude in the midfrontal electrode cluster. Delta

336   amplitude increased for abstraction and theta amplitude increased for set-size. However, beta-

337   band amplitude decreased for both higher abstraction and higher set size, but with a slightly

338   different spread in frequency within the beta-band. Peak beta amplitude modulation for the

339   abstraction contrast occupied a lower frequency range, from 12-18 Hz, compared to the wider

340   frequency range in peak beta amplitude modulation for the set-size contrast from 12-22 Hz.

341   In order to better understand the timecourse of amplitude modulations found for the

342   contrasts of interest, the time course for the amplitude of delta, theta and beta frequency bands

343   in the frontal midline cluster is plotted in Figure 4. Approximately 500 milliseconds after stimulus

344   onset, the high abstraction, high set-size condition showed the greatest delta amplitude

345   increase followed by high abstraction, low set-size and then both low abstraction conditions

346   (Figure 4A). Approximately 1200 to 1800 milliseconds after stimulus onset, the two high set-size

347   conditions showed an increase in theta amplitude (Figure 4B). Thus, both delta and theta

348   frequency bands showed increased amplitude sustained throughout stimulus processing for

349   greater abstraction or set-size. Finally, there was a decrease in amplitude in the beta frequency

350   band for all four conditions for the first 600 milliseconds (Figure 4C). However, only the high

351   abstraction, high set-size condition showed a significant and prolonged decrease in beta

352   amplitude relative to the other three conditions from 600 to 1600 milliseconds after stimulus

353   onset.

354   Since the stimulus-locked time-frequency effects persist after the probe for over a

355   second, it is possible that decreased beta amplitude was related to a systematic difference in

356   response time between conditions, and low-frequency activity in delta and theta band might only

357   be significantly elevated after a response is made reflecting post-response monitoring

358   processes. If decreased beta amplitude was indeed driven by motor-related processes, then it

359   would not be observed in a response-locked analysis. If low frequency activity reflects post-

360   response monitoring processes, then it would only be observed after the response in a

361   response-locked analysis. We performed a response-locked time-frequency analysis on the

362   abstraction and set-size contrast in the midfrontal electrode cluster (Figure 5). For the

363   abstraction contrast (Figure 5A), there was a significant decrease in amplitude in the beta

364   frequency band (10-20 Hz) just prior to a response, whereas there was no change in beta band

365   amplitude for the set-size contrast (Figure 5B). Thus, the modulation of beta amplitude by set-

366   size was most likely driven by a difference in response time, whereas the modulation of beta

367   amplitude as a function of task abstraction is more likely driven by stimulus processing. No

368   significant delta band amplitude was observed time-locked to the period just prior to the

369   response. For the set-size contrast (Figure 5B), there was a significant increase in amplitude in

370   the theta frequency band (3-8 Hz), starting at 1500 milliseconds prior to a response and

371   persisted after the response. Thus, the significant change in theta amplitude as a function of

372   set-size most likely does not only reflect post-response processes, but also related to pre-

373   response stimulus processing.

374

375   *Relationship between neuronal oscillations and behavior*

16

376   Next, we investigated whether the significant changes in spectral amplitude during

377   different task conditions correlated with behavior. To test this, we extracted spectral amplitude

378   values from the significant time-frequency clusters for the abstraction (2-3 Hz delta and 18-22

379   Hz beta; Figure 3A) and set-size (4-6 Hz theta and 18-22 Hz beta; Figure 3B) contrasts from the

380   frontal midline electrode cluster, since this cluster showed the strongest peak in these contrasts

381   (Figure 3C-F). We correlated the change in beta and delta amplitude with the change in RT as a

382   function of abstraction. RT was analyzed since accuracy was at ceiling for many participants.

383   For the abstraction contrast, task differences in beta band amplitude was significantly negatively

384   correlated with RT ($r(30)$ = -0.59, p = 0.001) and task differences in delta band amplitude was

385   significantly positively correlated with RT ($r(30)$ = 0.45, p = 0.012; Figure 6A). For the set-size

386   contrast, we correlated the change in beta and theta amplitude with the change in RT as a

387   function of task set-size. We found that the increase in theta band amplitude was significantly

388   positively correlated with RT ($r(30)$ = 0.36, p = 0.047), whereas there was no significant

389   relationship between beta band amplitude and behavior ($r(30)$ = -0.24, p = 0.20; Figure 6B). Our

390   time frequency results (Figure 3) found that peak beta amplitude decreased from 12-18 Hz by

391   abstraction and decreased from 12-22Hz by set-size. Therefore, we examined whether the

392   observed behavioral correlation was consistent for the high (18-22Hz) and low (12-18Hz) beta

393   bands. Just as with the high beta band, amplitude in the low beta band significantly negatively

394   correlated with abstraction ($r(30)$ = -0.47, p = 0.008) but did not show a significant relationship

395   with set-size ($r(30)$ = -0.15, p = 0.41). Thus, we do not find evidence that low and high beta

396   serve different functional roles. Altogether, increased delta and decreased beta amplitude

397   correlated with increased response time as a function of rule abstraction, and increased theta

398   amplitude correlated with increased response time as a function of task set-size.

399

400   *Phase Amplitude Coupling Results*

401   Our results thus far provide evidence that delta and beta oscillations may reflect the

402   cognitive processes related to increased abstraction, whereas theta may reflect the cognitive

403   processes related to increased set-size. To further probe the interactions between these

404   oscillations in different frequency bands, we conducted a phase amplitude coupling (PAC)

405   analysis. We investigated the coupling strength of the phase of the slower frequency bands,

406   delta and theta, with the amplitude of the higher frequency bands, beta and gamma. The

407   comodulograms for each condition were calculated for the phase of low frequencies (2-7 Hz) to

408   the amplitude of high frequencies (10-49 Hz) (Figure 7). Since both delta and beta amplitude

409   were modulated as a function of the abstraction of the task condition, we focused our statistical

410   analysis on the coupling between delta phase (2-3 Hz) coupled to beta amplitude (18-22 Hz).

411   Given that we found theta-gamma PAC in our previous electrocorticography study with a similar

412   task (Voytek, Kayser et al. 2015), we also analyzed coupling of the phase of the theta frequency

413   band (4-6 Hz) with the amplitude of the gamma frequency band (40-49 Hz). We found a

414   significant increase in delta-beta PAC with increased abstraction ($F(1,30) = 7.62$, $p = 0.00976$,

415    $\eta^2_p = 0.203$; Figure 7A,B), but not set-size ($F(1,30) = 2.63$, $p = 0.115$, $\eta^2_p = 0.0807$), and there

416   was no interaction ($F(1,30) = 2.79$, $p = 0.105$, $\eta^2_p = 0.0852$). For theta-gamma PAC, we found a

417   significant increase in PAC for the low abstraction conditions relative to the high abstraction

418   conditions ($F(1,30) = 4.56$, $p = 0.0409$, $\eta^2_p = 0.132$; Figure 7C,D), but no effect of theta-gamma

419   PAC for set-size ($F(1,30) = 1.16$, $p = 0.290$, $\eta^2_p = 0.0372$), and no interaction ($F(1,30) = 0.591$, p

420    $= 0.448$ $\eta^2_p = 0.0193$). During the high abstraction, high set-size condition, we found a

421   significant increase in delta-beta PAC ($t(30) = 2.377$, $p = 0.012$, $d = 0.427$), one-tailed; Figure

422   7B) and beta amplitude was strongest at the trough and rise of delta phase (Figure 8A). During

423   the low abstraction, high set-size condition, we found a moderate increase in theta-gamma PAC

424   ($t(30) = 1.665$, $p = 0.053$, $d = 0.299$, one-tailed; Figure 7D) and gamma amplitude was strongest

425   at the rise of theta phase (Figure 8B). Therefore, delta-beta coupling may be how low frequency

426   oscillations modulate high frequency oscillations to execute abstract rules, whereas theta-

427   gamma coupling may be relevant for maintaining task rules with higher set size.

428

429   **Discussion**

430

431   In this experiment, we investigated the oscillatory neural dynamics associated with two

432   dissociable components of hierarchical cognitive control: rule abstraction and set-size. Previous

433   studies found that various frequency bands from low frequency delta to high frequency gamma

434   are associated with cognitive control (Helfrich and Knight 2016), but the specific contribution of

435   each of these bands to different control processes remains underspecified. We found that the

436   abstraction and set-size of task rules are each associated with distinct oscillatory mechanisms.

437   Specifically, when the abstractness of the rule increased, delta amplitude increased and beta

438   amplitude decreased; whereas when the number of rules (set-size) increased, theta amplitude

439   increased and beta amplitude decreased. These task-dependent changes in oscillatory

440   amplitude correlated with behavioral performance. When the abstraction of the rule increased,

441   slower response times correlated with increased delta amplitude and decreased beta amplitude.

442   When the set-size increased, slower response times correlated with increased theta amplitude.

443   Prior to the motor response, increased abstraction decreased beta amplitude, and increased

444   set-size increased theta amplitude. Finally, coupling between the phase of delta oscillations and

445   the amplitude of beta oscillations strengthened as a function of task abstraction.

446   Cognitive control is organized hierarchically such that superordinate abstract

447   representations influence subordinate, concrete action representations. In our previous study

448   using electrocorticography with a similar version of the task (Voytek, Kayser et al. 2015), we

449   found that tasks that engaged more abstract task rules increased theta synchrony between the

450   prefrontal cortex (PFC) and premotor cortex. Furthermore, we found theta phase in the PFC

451   coupled with gamma amplitude in premotor regions, suggesting that the PFC communicates

452   with the motor cortex for hierarchical control via theta-gamma phase amplitude coupling

453   (Voytek, Kayser et al. 2015). However, one important limitation of this previous study is that

454   tasks that required more abstract rules also had increased set-size; therefore, we could not

455   discern whether changes in oscillatory activities were driven by differences in abstraction or set-

456   size. An important feature of our current experiment was to separately manipulate the

457   abstraction of the rule and the number of competing rules (set-size). We further matched the

458   performance (accuracy) between high and low abstraction. Therefore, we were able to

459   dissociate these two components of hierarchical cognitive control.

460   Our findings suggest a relationship between theta oscillations and set-size, and this

461   finding is consistent with previous studies that reported theta oscillations scale with working

462   memory load (Jensen and Tesche 2002, Meltzer, Negishi et al. 2007, So, Wong et al. 2017,

463   Berger, Griesmayr et al. 2019). Other studies have also found that theta oscillations

464   (presumably from frontal cortex) increase during tasks that required cognitive control (Cohen

465   2011, Hsieh, Ekstrom et al. 2011, Kikumoto and Mayr 2018). Theta-gamma coupling has been

466   suggested as a mechanism by which multiple representations are organized for working

467   memory (Bahramisharif, Jensen et al. 2018) and long-term memory (Heusser, Poeppel et al.

468   2016). Therefore, the increased theta-gamma PAC for higher set-size in our task could reflect

469   the maintenance or retrieval of an increased number of rules. It should be noted that in our

470   previous study using electrocorticography, we found increased theta phase to high gamma

471   amplitude coupling for the high abstraction, high set-size condition (Voytek, Kayser et al. 2015).

472   While we were unable to measure theta to high gamma coupling due to the limitations of EEG,

473   we did find increased theta amplitude for this condition consistent with these findings.

474   Furthermore, this previous study did not separately manipulate abstraction and set-size, which

475   we investigated in the current study (see Methods).

476   We observed that beta amplitude decreased after stimulus onset as a function of

477   increased abstraction and increased set-size. For the response-locked analysis, beta

478   oscillations decreased only as a function of increased abstraction, but not increased set-size.

479   Many studies have found that beta oscillations decrease when the motor system executes an

480   action (Little and Brown 2012). While we also observed that beta band amplitude decreased

481   before the button press, higher abstraction conditions showed a greater beta amplitude

482   decrease when compared to lower abstraction conditions. We also found decreased beta

483   amplitude as a function of abstraction in the stimulus-locked analysis. Together, these

484   abstraction dependent results indicate a role for beta oscillations beyond motor preparation. We

485   propose that beta oscillations may reflect top-down inhibitory signals for guiding action that are

486   most robustly disengaged when guided by hierarchical goal representations.

487   Our findings of increased delta and decreased beta oscillations with increased

488   abstraction are consistent with a previous study that examined performance of a delayed-

489   match-to-sample task in which monkeys had to evaluate an object according to two different

490   categorical judgements: left versus right or up versus down (Antzoulatos and Miller 2016). This

491   study reported that distinct neural populations carry information for each of these two

492   categories: vertically selective populations and horizontally selective populations. For the cued

493   category, beta coherence increased between the neural populations that coded for the relevant

494   category. This pattern of activity led the authors to conclude that beta oscillations were encoding

495   rule categories. Our task also required the maintenance of abstract rules and similarly found an

496   abstraction-related modulation of beta amplitude in prefrontal cortex. Furthermore, when there

497   was a shift in the boundary between what was defined as "up" and "down," there was an

498   increase in delta synchrony between prefrontal and parietal cortex. This suggests that updates

499   to abstract categorical rules modulates delta oscillations. In our experiment, for the high

500   abstraction, high set-size condition, participants had to evaluate the similarity of two different

501   objects based on different stimuli attributes (e.g., judge the similarity in texture or shape), and

502   the relevant attribute that participants should focus on was instructed by a supraordinate task

503   rule cued by the color of the square surrounding the stimuli. Based on the findings from

504 Antzoulatos & Miller 2016, the increase in delta oscillations in our study may reflect an update to

505 the relevant supraordinate rule, and the change in beta oscillations may reflect rule selection.

506 Participants with the greatest increase in response time when responding to the

507 increased abstraction conditions showed the greatest increase in delta amplitude and decrease

508 in beta amplitude. Similarly, participants with the greatest increase in response time when

509 responding to the increased set-size conditions showed the greatest increase in theta

510 amplitude. These findings emphasize the behavioral relevance of these low frequency neuronal

511 oscillations and provide further support for a role of delta oscillations in processing task

512 abstraction and theta oscillations in processing increased set-size.

513 The interplay between slow and fast neuronal oscillations has been investigated as a

514 mechanism for cognitive control (Sauseng, Klimesch et al. 2009, Sauseng, Griesmayr et al.

515 2010, Roux, Wibral et al. 2012, Voytek, Kayser et al. 2015) as long-range, low frequency

516 cognitive control signals from prefrontal cortex couple to more local high frequency oscillations

517 (Canolty and Knight 2010, Sauseng, Griesmayr et al. 2010). Our PAC analysis revealed that

518 delta phase coupled with beta amplitude when task conditions became more abstract.

519 Specifically, delta-beta coupling increased in the high abstraction, high set-size condition in

520 which participants decide between two task rules (e.g., focus on texture or shape). We observed

521 that beta amplitude decreased around the peak of the delta phase (see Figure 8A). This finding

522 is similar to Helfrich et al. (2017) in which alpha-beta amplitude was lowest at peak delta-phase

523 in prefrontal cortex during a perceptual judgement (Helfrich, Huang et al. 2017). Wyart et al.

524 (2012) also reported that the distribution of beta oscillations in motor cortex was updated every

525 cycle of a prefrontal delta signal, and the amplitude of beta was inversely related to the

526 probability of action of the underlying motor cortex (Wyart, de Gardelle et al. 2012). Consistent

527 with Wyart et al. 2012, our PAC finding suggests that delta phase in frontal regions may guide

528 action selection via modulating beta-band amplitude when cognitive tasks are hierarchically

529 organized, and participants have to rely on supraordinate, abstract rules to guide concrete

530 actions.

531   Taken together, low frequency oscillations in the theta and delta frequency band may

532 reflect different components of hierarchical cognitive control that couple to different high

533 frequency oscillations. Gamma oscillations play a primary role in carrying feedforward sensory

534 processing signals (Börgers and Kopell 2008, Michalareas, Vezoli et al. 2016). Theta

535 oscillations in prefrontal cortex couple with gamma oscillations to support the organization of

536 perceptual information during memory encoding and retrieval (Osipova, Takashima et al. 2006,

537 Hsieh and Ranganath 2014). When multiple items must be held in mind, theta-gamma coupling

538 is increased (Alekseichuk, Turi et al. 2016, Tamura, Spellman et al. 2017, Bahramisharif,

539 Jensen et al. 2018). Our findings suggest that increasing the set-size of a task may recruit a

540 similar neural mechanism. Beta oscillations play a role in sensory feedback (Bastos, Vezoli et

541 al. 2015, Michalareas, Vezoli et al. 2016) and motor control (Zhang, Chen et al. 2008, Picazio,

542 Veniero et al. 2014). Therefore, delta to beta coupling may be a mechanism by which low

543 frequency oscillations in prefrontal cortex guide future action according to abstract goals.

544 Theoretical models on the role of gamma and beta oscillations in bottom-up and top-down

545 attention (Fries 2015, Riddle, Hwang et al. 2019) may be extended to include theta and delta

546 oscillations that show task-related modulations in the frontal cortex.

547

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702

703   **Figure 1**. **Hierarchical cognitive control task**

704   (A) The hierarchical cognitive control task used a two by two design with four conditions. On the

705   X-axis, the set-size increases within a fixed level of abstraction. On the Y-axis, the level of

706   abstraction increases. Behavioral results for response time (B) and accuracy (C). Error bars are

707   S.E.M.

708

709   **Figure 2**. **Electrode clusters used for EEG analysis**

710   Hierarchical clustering of the time-frequency data for each electrode revealed six distinct

711   electrode clusters. The analysis focused on the frontal midline electrode cluster

712   (outlined). The other electrode clusters were used for cluster-mass permutation testing in

713   time-frequency analysis.

714

715   **Figure 3. Time-frequency analysis of hierarchical cognitive control along two**

716   **dimensions: abstraction and set-size**

717   In the frontal-midline electrode cluster, there was a significant increase in delta and

718   decrease in beta amplitude as a function of task abstraction (A). The dark outline

719   highlights time-frequency clusters that were found to be significant at $p < 0.05$ and

720   survived correction for multiple comparisons. Delta amplitude increase was localized to

721   the frontal-midline and right frontal (B). Beta amplitude decrease was localized to the

722   frontal- and central-midline (C). In the frontal-midline electrode cluster, there was a

723   significant increase in theta amplitude and decrease in beta amplitude as a function of

724   task set-size. The increase in theta amplitude was localized to the frontal-midline

725   electrodes (E). The decrease in beta amplitude was localized to frontal-midline

726   electrodes (F).

727

728   **Figure 4. Time course of task-evoked oscillatory amplitude**

729   At time 0, the stimulus for the task is presented. (A) Delta amplitude showed the greatest

730   increase in the two high abstraction conditions (red and orange). (B) Theta amplitude

731   showed the greatest in the response task (dark blue and light blue) in the first 0.5

732   seconds and the greatest increase in the high set-size conditions (dark blue and red) in

733   the 1 to 2 second range. (C) Beta amplitude showed the greatest decrease in the high

734   abstraction, high set-size condition (red). Error bars are S.E.M.

735

736   **Figure 5. Response-locked time frequency analysis**

737   The response-locked time frequency analysis for the abstraction (A) and set-size (B)

738   contrast in the midfrontal electrode cluster found a significant decrease in low beta

739   amplitude prior to response for abstraction and increase in theta amplitude prior to and

740   after response for set-size. The line at time 0 is the time that the participant made a

741   response. The dark outline highlights time-frequency clusters that were found to be

742   significant at $p < 0.05$ with a cluster correction of $k = 100$.

743

744   **Figure 6. Behavior to brain correlations**

745   Correlation analysis for response time to spectral density for the significant clusters in

746   abstraction (A) and set-size (B). Error bars are 95% confidence intervals. * $p < 0.05$, ** p

747   < 0.005, n.s. = not significant.

748

749   **Figure 7**. **Comodulograms of phase amplitude coupling for each task condition**

750   For the high abstraction conditions, there was increased coupling between delta phase

751   (2-3 Hz) and beta amplitude (18-22 Hz) in the high-set (B), but not low set-size condition

752   (A). For the low abstraction conditions, there was increased coupling between theta

753   phase (4-6 Hz) and gamma amplitude (40-49 Hz) in the low and high set-size conditions
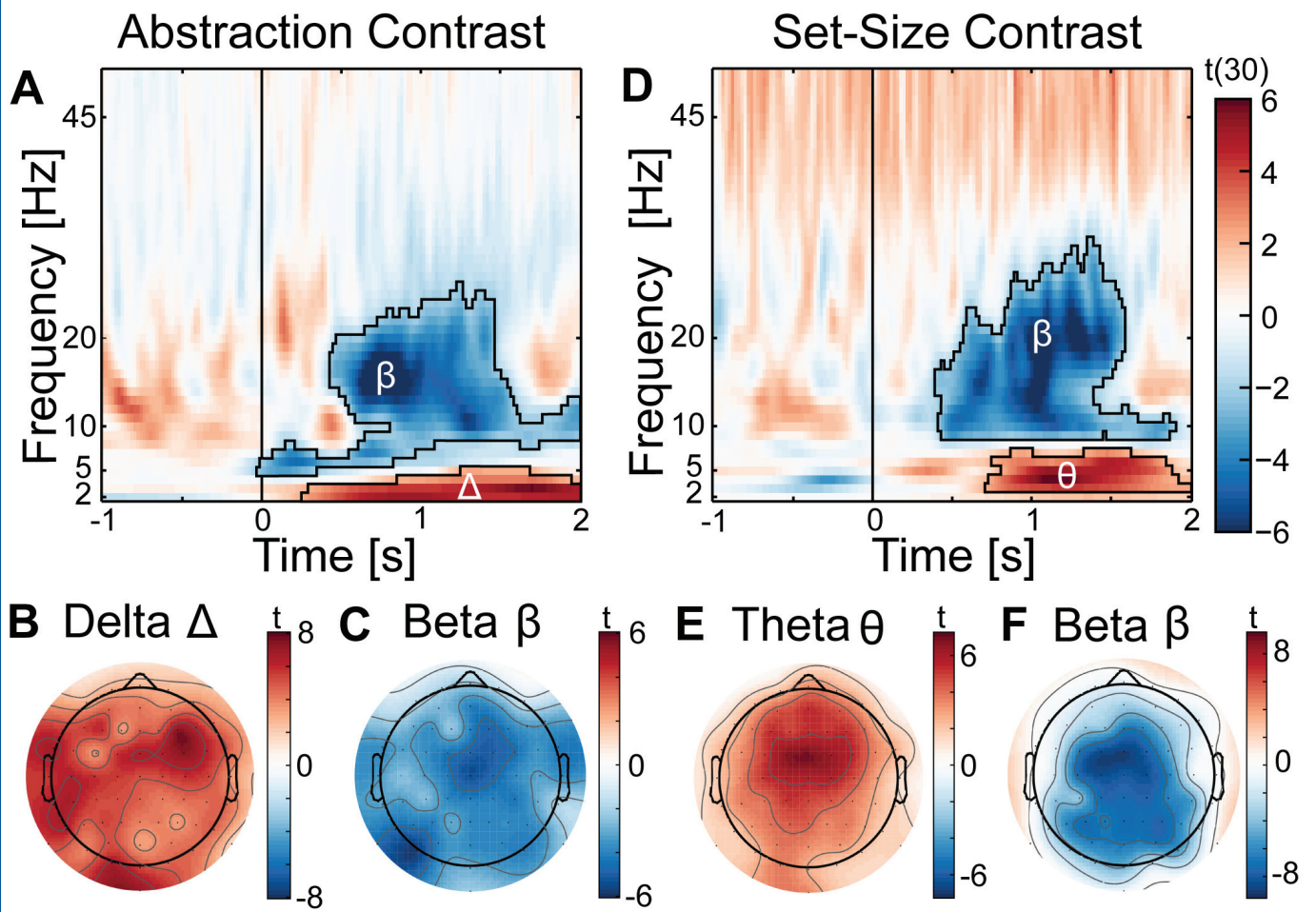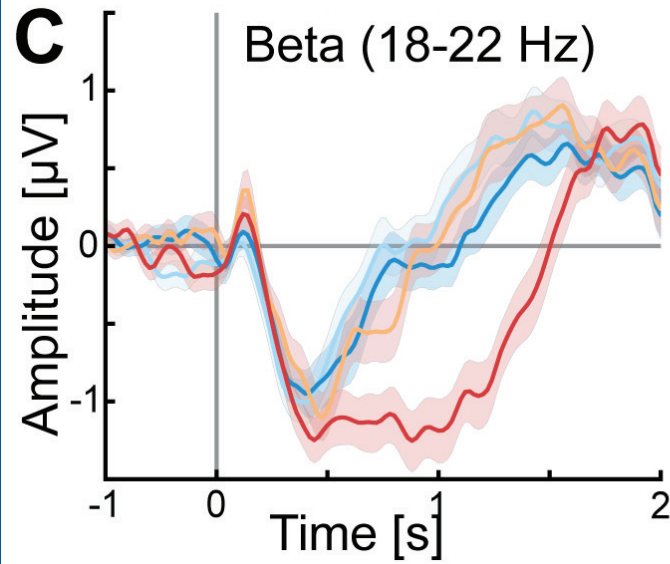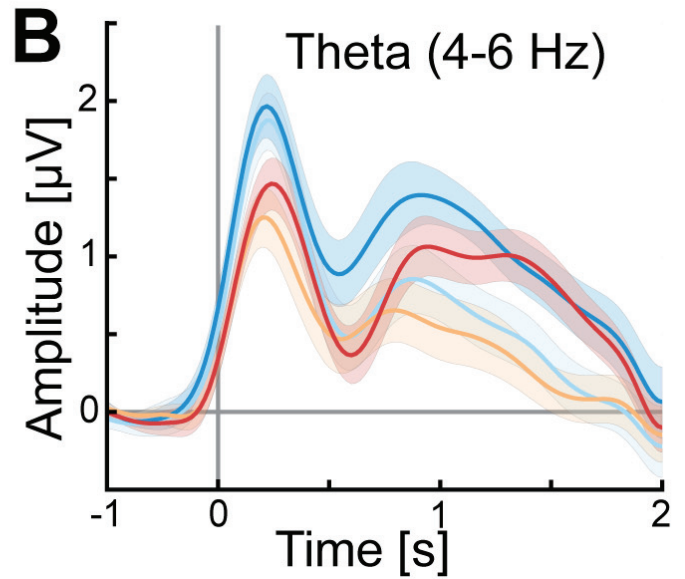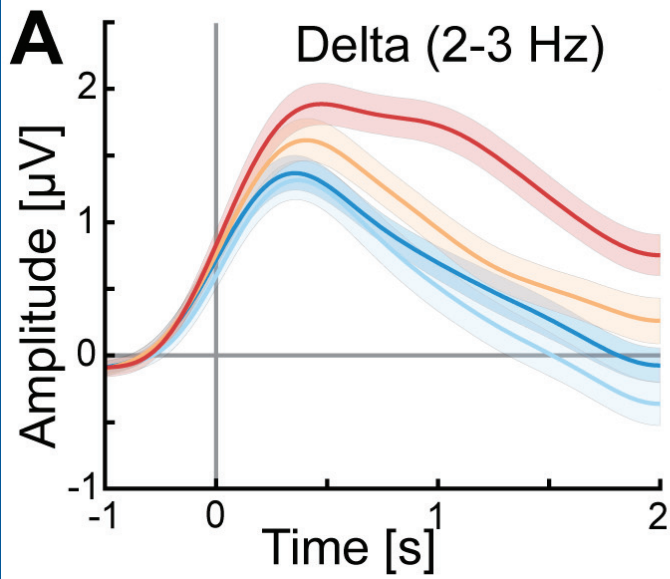
754   (C, D).

755

756   **Figure 8. Distribution of beta and gamma amplitude across delta and theta phase**

757   Rose plots of delta phase coupled to beta amplitude (A) for the high abstraction, high

758   set-size condition and theta phase coupled to gamma amplitude (B) for the low

759   abstraction, high set-size condition. Amplitude values (z) were binned into 30 phase

760   angles, averaged, and z-scored across phase bins. Error bars are within-participant

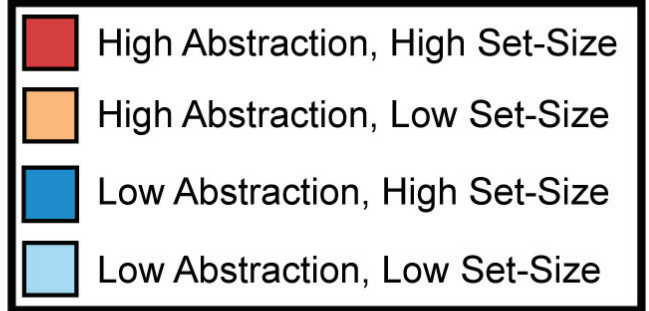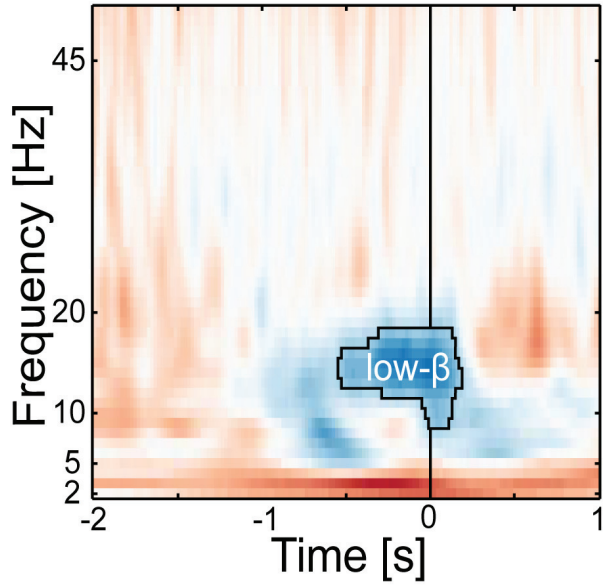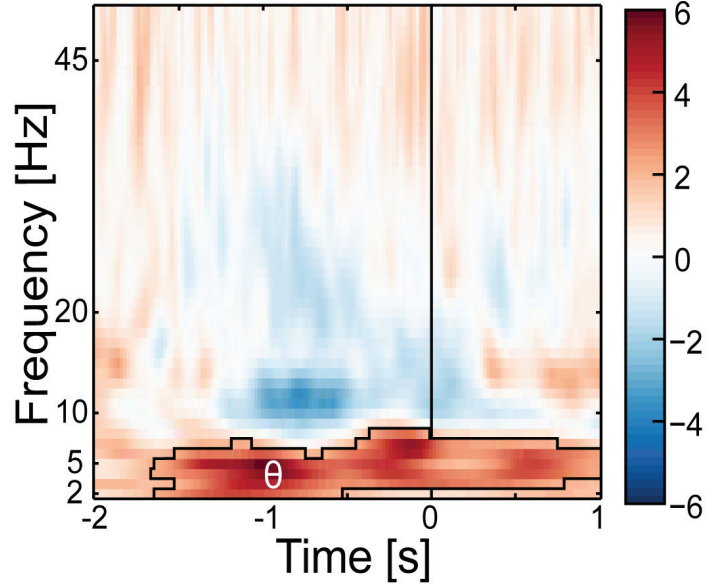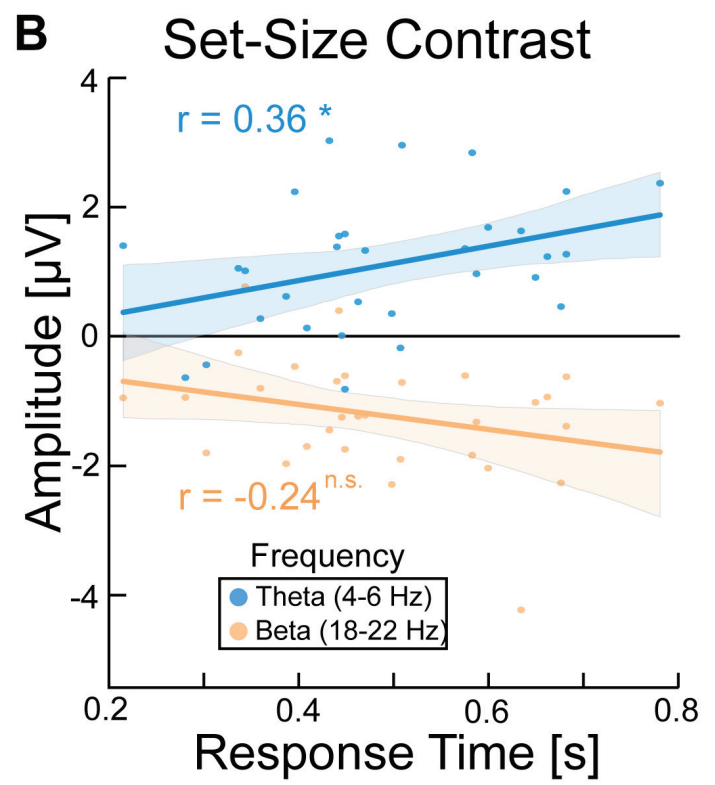761   SEM. Legends depict the peak and trough values in radians.

Abstraction Contrast

A Frequency [Hz] — β, Δ — Time [s]

Set-Size Contrast

D Frequency [Hz] — β, θ — Time [s] — t(30)

B Delta Δ   t

C Beta β   t

E Theta θ   t

F Beta β   t

A Delta (2-3 Hz)

B Theta (4-6 Hz)

C Beta (18-22 Hz)

Task Condition

High Abstraction, High Set-Size
High Abstraction, Low Set-Size
Low Abstraction, High Set-Size
Low Abstraction, Low Set-Size
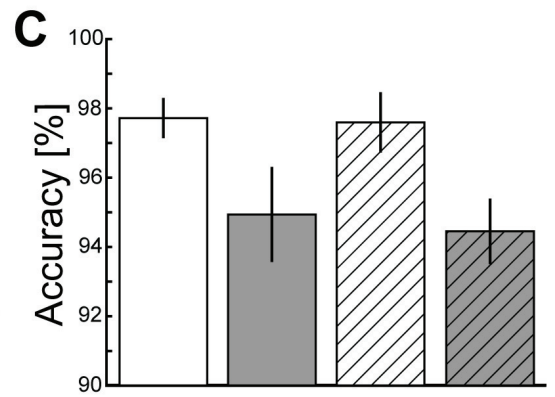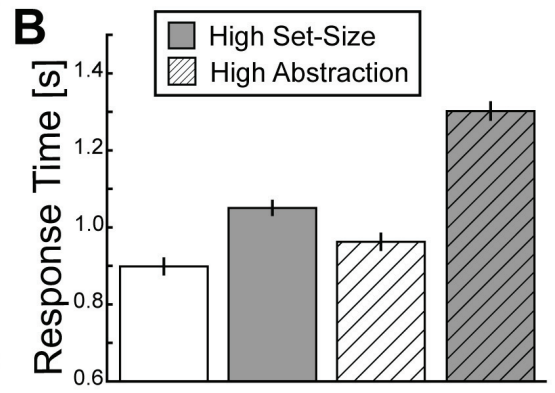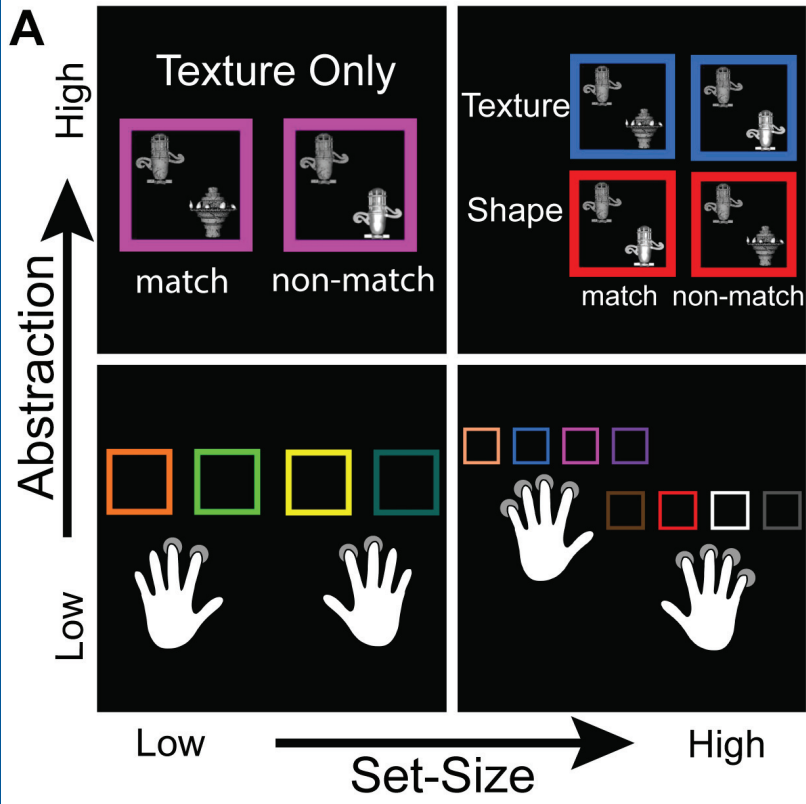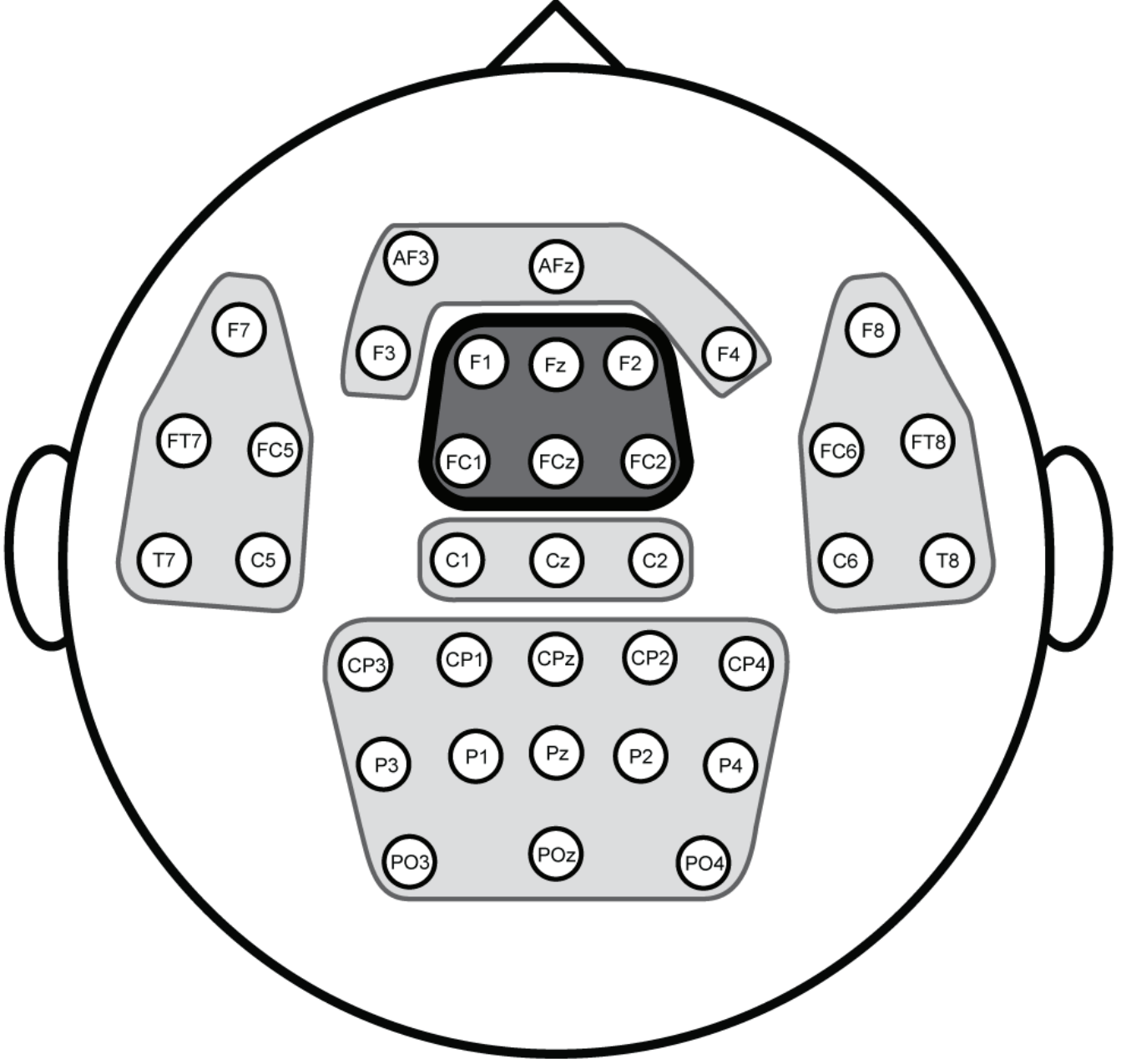
A Abstraction Contrast

B Set-Size Contrast

A Abstraction Contrast

r = 0.45 *

r = -0.59 **

Amplitude [μV]

Response Time [s]

Frequency
- Delta (2-3 Hz)
- Beta (18-22 Hz)

B Set-Size Contrast

r = 0.36 *

r = -0.24 n.s.

Amplitude [μV]

Response Time [s]

Frequency
- Theta (4-6 Hz)
- Beta (18-22 Hz)
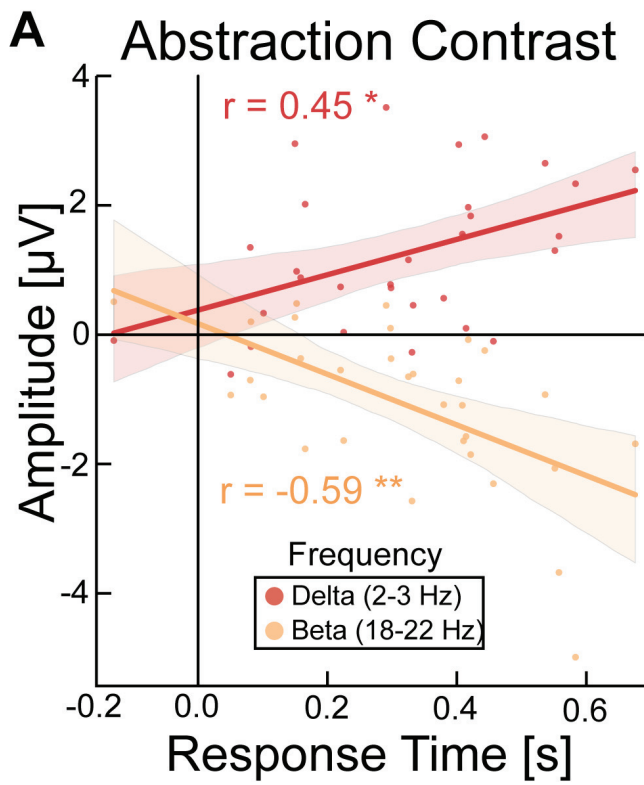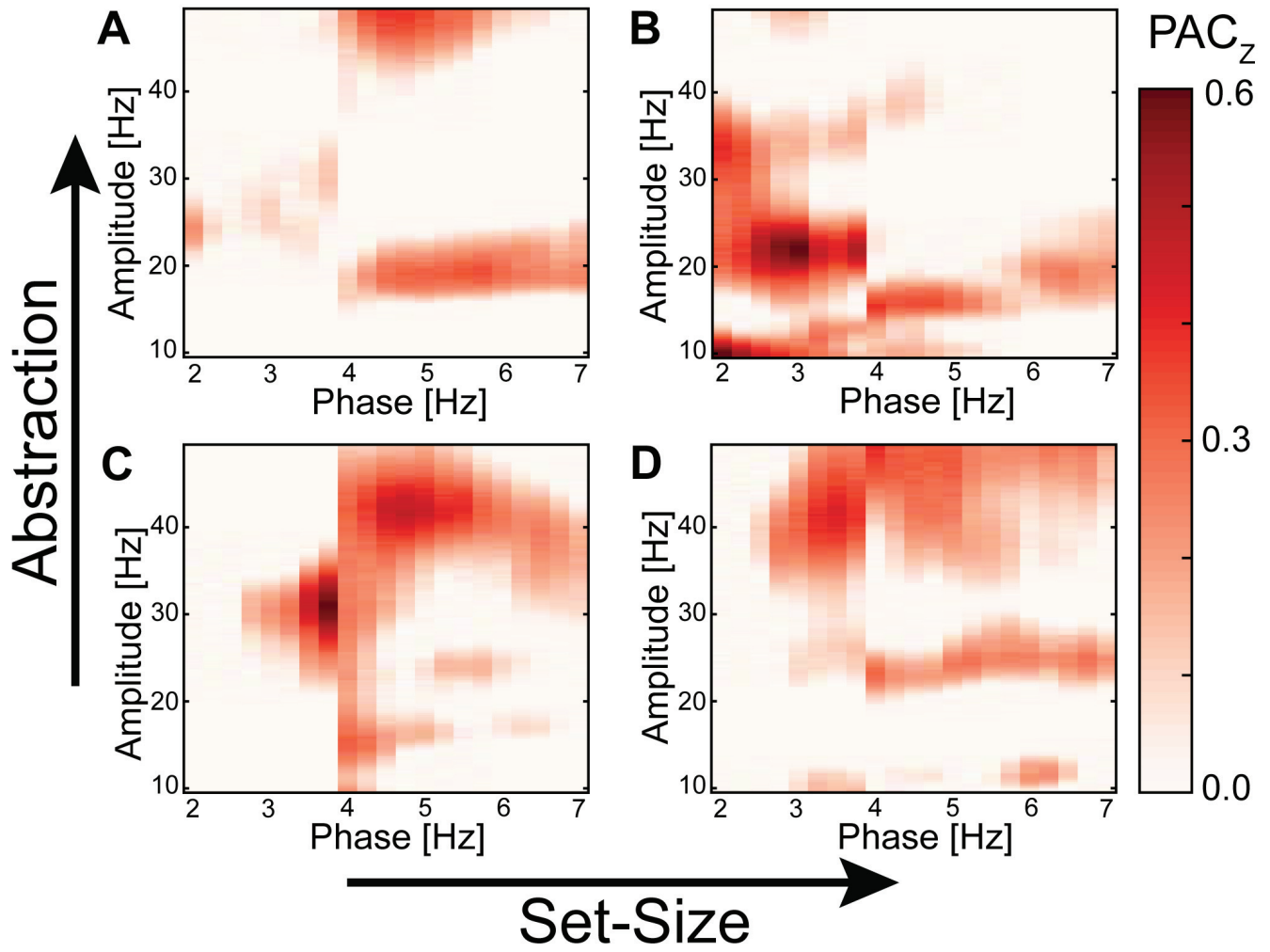
A Delta-Beta (2-3, 18-22)

B Theta-Gamma (4-6, 40-49)