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**Research Articles: Behavioral/Cognitive**

**Cortical oscillatory mechanisms supporting the control of human social-emotional actions**

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Cortical oscillatory mechanisms supporting the control of human social-emotional actions

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36 **Abstract**

37           The human anterior prefrontal cortex (aPFC) is involved in regulating social-emotional  
38 behavior, presumably by modulating effective connectivity with down-stream parietal, limbic, and  
39 motor cortices. Regulating that connectivity might rely on theta-band oscillations (4-8 Hz), a brain  
40 rhythm known to create overlapping periods of excitability between distant regions by temporally  
41 releasing neurons from inhibition. Here, we use magnetoencephalography (MEG) to understand how  
42 aPFC theta-band oscillations implement control over prepotent social-emotional behaviors, i.e. the  
43 control over automatically elicited approach and avoidance actions.

44           Forty human male participants performed a social approach-avoidance task, in which they  
45 approached or avoided visually displayed emotional faces (happy or angry) by pulling or pushing a  
46 joystick. Approaching angry and avoiding happy faces (incongruent condition) requires rapid  
47 application of cognitive control to override prepotent habitual action tendencies to approach  
48 appetitive and to avoid aversive situations. In the time window prior to response delivery, trial-by-  
49 trial variations in aPFC theta-band power (6 Hz) predicted reaction time increases during emotional  
50 control, and were inversely related to beta-band power (14-22 Hz) over parieto-frontal cortex. In  
51 sensorimotor areas contralateral to the moving hand, pre-movement gamma-band rhythms (60-90  
52 Hz) were stronger during incongruent than congruent trials, with power increases phase-locked to  
53 peaks of the aPFC theta-band oscillations.

54           These findings define a mechanistic relation between cortical areas involved in implementing  
55 rapid control over human social-emotional behavior. The aPFC may bias neural processing towards  
56 rule-driven actions and away from automatic emotional tendencies by coordinating tonic  
57 disinhibition and phasic enhancement of parieto-frontal circuits involved in action selection.

58

59 **Significance statement**

60 Being able to control social-emotional behavior is crucial for successful participation in society, as is  
61 illustrated by the severe social and occupational difficulties experienced by people suffering from  
62 social motivational disorders, such as social anxiety. In this study, we show that theta-band  
63 oscillations in the aPFC, which are thought to provide temporal organization for neural firing during  
64 communication between distant brain areas, facilitate this control by linking aPFC to parieto-frontal  
65 beta-band and sensorimotor gamma-band oscillations involved in action selection. These results  
66 contribute to a mechanistic understanding of cognitive control over automatic social-emotional  
67 action, and point to frontal theta-band oscillations as a possible target of rhythmic neurostimulation  
68 techniques during treatments of social anxiety.

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81 **Introduction**

82 Human cooperative social environment relies on our ability to control social-emotional  
 83 behavior (Hare, 2017). The importance of this ability is illustrated by conditions in which this control  
 84 fails. For instance, in social anxiety disorder, persistent avoidance of social interactions causes  
 85 impairment in social and occupational functioning (Clark and Wells, 1995; Craske and Stein, 2016).  
 86 Social-emotional disorders also illustrate how regulating social-emotional behavior requires more  
 87 than suppressing automatic emotional action tendencies. In fact, social-emotional regulation is an  
 88 action selection feat, involving the selection of adequate behaviors from numerous potential  
 89 strategies, while anticipating the consequences of those behaviors in other agents. For example, in a  
 90 job-interview, applicants might make it more likely to get the job when they overcome their  
 91 tendency to avoid the test and dare to approach when asked who will present first. These  
 92 emotionally-laden counterfactual computations are thought to be implemented by the anterior  
 93 prefrontal cortex (aPFC; Daw et al., 2006; Boorman et al., 2009; Volman et al., 2013), a region also  
 94 known to influence downstream neural activity in the amygdala and posterior parietal cortex (PPC)  
 95 during emotional action control (Mars et al., 2011; Volman et al., 2011a, 2013, 2016). However, the  
 96 neural mechanisms that support social-emotional regulation across this network remain unclear. In  
 97 this study, we use neural oscillations as a metric for understanding how aPFC rapidly selects and  
 98 implements alternative courses of action over prepotent habitual social-emotional behaviors.

99 Recent studies have shown that implementation of prefrontal control is often rhythmic,  
 100 transferring information between regions through entrainment of neural oscillations (Helfrich and  
 101 Knight, 2016). aPFC neurons tend to phase-lock their spiking and gamma-band firing to the theta-  
 102 band rhythm (4-8 Hz) (Ardid et al., 2015; Voytek et al., 2015). Frontal theta-band oscillations have  
 103 been consistently involved in control over motivational behavior (Cavanagh and Frank, 2014; Cooper  
 104 et al., 2015), including control over state-induced affective behavioral biases (Cavanagh et al., 2013)  
 105 and feedback-related control in exploration behavior (Cavanagh et al., 2011). Theta-band oscillations  
 106 might support emotional control by temporally orchestrating release of neurons from inhibition, thus

107 creating overlapping periods of excitability across the cerebral network involved in social-emotional  
 108 regulation (Colgin, 2013; Lisman and Jensen, 2013; Volman et al., 2013). Human aPFC has extensive  
 109 anatomical connections with portions of the PPC (Mars et al., 2011; Neubert et al., 2014), and aPFC-  
 110 PPC effective connectivity relies on theta-band rhythm modulations (Phillips et al., 2013; Karalis et  
 111 al., 2016). Here we test whether social-emotional action tendencies are controlled through theta-  
 112 band oscillations. We explore the dynamics of interactions between theta-band oscillations in aPFC  
 113 and the beta/gamma rhythms produced by posterior areas during action selection.

114 We measured neural activity in forty human participants using magnetoencephalography  
 115 (MEG), while they performed a social approach-avoidance (AA) task. In this task, participants  
 116 approach or avoid visually-displayed emotional faces by pulling or pushing a joystick, respectively.  
 117 Approaching angry and avoiding happy faces requires implementing rapid control to override  
 118 automatic tendencies to approach appetitive and avoid aversive situations. This complex form of  
 119 control operates on the interaction between the emotional valence of percepts and actions, and it is  
 120 modulated by social psychopathologies and socially-relevant hormones (Heuer et al., 2007; von  
 121 Borries et al., 2012; Radke et al., 2013, 2017; Enter et al., 2016).

122 Previous fMRI studies have shown that during affect-incongruent trials, aPFC and PPC activity  
 123 is increased, and amygdala activity decreased, suggesting that the aPFC exerts control over social-  
 124 emotional actions, possibly by interacting with PPC to assist in action selection (Rowe et al., 2008;  
 125 Volman et al., 2011a). Building on those fMRI and electrophysiological observations, we predict that  
 126 the emotional control evoked during incongruent trials will result in stronger theta-band power in  
 127 aPFC. We also explore whether theta-band oscillations over aPFC are coupled to rhythms involved in  
 128 action selection, i.e. beta- and gamma-band rhythms over parieto-frontal areas (De Lange et al.,  
 129 2008; Jenkinson and Brown, 2011; Brinkman et al., 2014; Voytek et al., 2015).

## 130 **Materials and Methods**

### 131 *Participants*

132 Forty-five undergraduate students from the Radboud University took part in the experiment.  
 133 Five participants did not complete the experiment, with three participants failing to follow task  
 134 instructions (>30% error trials), and two participants showing substantial noise in the MEG data.  
 135 Forty participants were considered for analyses (mean age: 23.5, sd: 2.8, range: 18-33 years). All  
 136 participants signed an informed consent prior to the study and were compensated with monetary  
 137 reward or research credits. Before inclusion, participants were screened for epilepsy and history of  
 138 mental illness. All participants were males, right handed and had normal or corrected-to-normal  
 139 vision. The study was approved by the local ethical committee (CMO:2014/288).

### 140 *Materials and apparatus*

141 The task was programmed using Presentation software version 16.4 (neurobs.com;  
 142 RRID:SCR\_002521). Stimuli were presented using a PROPixx beamer with a refresh rate of 120 Hz and  
 143 a resolution of 1920:1080. MEG was acquired using a whole brain CTF-275 system with axial  
 144 gradiometers. Data were sampled at 1200 Hz after a 300 Hz lowpass filter was applied. Four sensors  
 145 (MLF62, MLC32, MLC11 & MRF66) were permanently disabled due to high noise. The helmet was set  
 146 at 15° and the participants were seated 80 cm from the screen. Head location was measured using  
 147 localization coils in both ear canals and on the nasion and was continuously monitored using online  
 148 head localization software (Stolk et al., 2013). In case of large deviations from the initial head  
 149 position (+5 mm) we paused the experiment and instructed the subject to move back to the original  
 150 position. During the task, participants responded using a customized Fiber Optic Joystick (fORP  
 151 design), that was calibrated for each participant prior to the experiment. A displacement of 20%  
 152 away from the center in the sagittal plane was taken as a response.



153 Participants performed an approach-avoidance (AA) task which has been used in several  
 154 previous studies (e.g. Volman et al., 2011), and was adapted for MEG; figure 1A. Trials started with  
 155 the presentation of a white fixation cross presented in the center of a black screen for 1000 ms. After  
 156 fixation, a face was presented for 100 ms, after which the subject had 2000 ms to respond by pushing  
 157 the joystick away, or pulling it towards themselves. Participants received written instructions on  
 158 screen before each block of 12 trials, in which they were instructed to push the joystick towards or  
 159 away from themselves for happy or angry faces respectively (congruent block), or towards/away  
 160 from themselves for angry/happy faces (incongruent block). These response rules alternated each  
 161 block. The task consisted of 16 blocks, yielding 196 trials in total. Stimuli consisted of equiluminant  
 162 faces that were presented at the center of the screen at a visual angle of 4.3 by 6.4 degrees. In  
 163 contrast to cognitive control tasks involving conflict on the stimulus level, such as emotional Stroop  
 164 tasks -typically implicating anterior cingulate cortex-, conflict between emotional percepts and  
 165 emotional actions such as mapped by the AAT is typically processed by higher order brain regions  
 166 such as the aPFC (Volman et al., 2011a).

167 High-resolution anatomical MRI images were acquired with a single-shot MPRAGE sequence  
 168 (acceleration factor 2 with GRAPPA method, TR 2400ms/TE2.13ms, effective voxel size 1 x 1 x 1mm,  
 169 176 sagittal slices, distance factor 50%, flip angle 8 degrees, orientation A >> P, FoV 256mm). To align  
 170 structural MRI to MEG we provided the participants with vitamin-E capsules in the ears, on the same  
 171 locations as the localizer coils in the MEG system.

## 172 *Procedure*

173 Upon arrival, participants received verbal task instructions before changing into non-  
 174 magnetic clothing. Prior to the experiment participants provided a saliva sample, enabling the  
 175 quantification of hormone levels for other research purposes. Once in the scanner, participants  
 176 performed a practice session containing 4 blocks of 8 trials each, using faces of different identity  
 177 from those displayed in the main experiment. Following the main session of the AA task, participants

178 provided a second saliva sample and completed the State Trait Anxiety Inventory (Spielberger et al.,  
 179 1970). Structural MRI was acquired in a separate session where participants also performed the AA  
 180 task using fMRI. fMRI and hormonal data are not reported here.

#### 181 *Behavioral analysis*

182 Reaction time analyses were performed on correct responses only. We removed trials in  
 183 which the reaction time exceeded a threshold of three standard deviations above or below the mean  
 184 reaction time of the subject for each condition separately (1.6 % of trials). Congruency effects in  
 185 reaction times and error rates were computed by subtracting congruent from incongruent trials.

#### 186 *MEG preprocessing*

187 MEG analyses were performed using Matlab2015a (the Mathworks; RRID:SCR\_001622),  
 188 Fieldtrip toolbox (Oostenveld et al., 2011) and custom written analysis scripts. After epoching the  
 189 data into trials ranging from -3 s before, until 1 s after response, we removed the third order  
 190 gradient. The trials were detrended and demeaned in order to remove slow drifts and non-zero DC  
 191 offset, and filtered using a discrete Fourier transform (DFT) filter to remove the 50 Hz line noise and  
 192 100 and 150 Hz harmonics. Next, we performed manual trial rejection to remove trials with large  
 193 deviations or artifacts. Independent component analysis (Makeig et al., 1996) was performed to  
 194 remove components that contained sources of noise (e.g. heartbeat, eye-blink, joystick artifacts).  
 195 After this step, all trials were visually inspected to remove any trial still containing large amounts of  
 196 noise. For the sensor-level analysis, we interpolated sensors that were missing due to noise removal  
 197 using a weighted average of neighboring sensors; for some sensors (N=8) this was not possible due to  
 198 removal of too many neighbors. Sensor level analyses were performed on 263 sensors.

#### 199 *Spectral Analysis*

200 To facilitate interpretation of the topographical distribution of signal resulting from the CTF  
 201 axial gradiometers, we calculated spectral power for the horizontal and vertical components of the

202 estimated planar gradient on each sensor location, which we then summed (Bastiaansen and  
 203 Knösche, 2000). This representation of the data ensures that power of a source is strongest just  
 204 above that source (Hämäläinen et al., 1993).

205 Time-frequency representations (TFR) of power were estimated in two steps. For frequencies  
 206 below 40 Hz, we used Short-time Fourier transform with sliding windows of 500 ms, multiplied with a  
 207 Hanning taper and moving in steps of 50 ms. The frequency resolution was 2 Hz. We pre-specified 6  
 208 Hz as theta-band and 14-22 Hz as beta-band activity. Theta-band definition was based on a-priori  
 209 expectations (Phillips et al., 2013; Cavanagh and Frank, 2014; Cooper et al., 2015; Karalis et al., 2016).  
 210 Beta-band definition was based on the congruency effect observed over all sensors. For frequencies  
 211 above 40 Hz (gamma-band; 40-130 Hz), we used three orthogonal Slepian tapers and sliding time  
 212 windows of 200 ms (moving in steps of 50 ms), creating frequency smoothing of approximately 10 Hz  
 213 (frequency resolution of 10 Hz; Percival and Walden, 1993). In the gamma-band analyses, we  
 214 identified changes in power evoked before response [-1000 until 0 ms], as compared to a baseline  
 215 period occurring before stimulus presentation (average of -800 until -500 ms). This procedure  
 216 increased statistical power by narrowing the frequency search space. The frequency band showing  
 217 increased power (60-90 Hz) was used in further (orthogonal) comparisons between conditions. With  
 218 the exception of single-trial analyses, all analyses were focused on the contrast between incongruent  
 219 and congruent conditions.

#### 220 *Source analyses*

221 Congruency effects were localized using DICS beamforming (Groß et al., 2001). We computed  
 222 a single-shell head model (Nolte, 2003) for each subject using anatomical MRI. Next, we warped the  
 223 individual MRI images to a template grid in MNI space (spatial resolution of 8 mm). To reconstruct  
 224 activity in the interval 0.5 s prior to response delivery (period of action selection, see results), we  
 225 used a Hanning taper followed by a Fourier transform centered at 6 Hz; and three orthogonal Slepian  
 226 tapers for beta-band (center frequency 18 Hz) and gamma-band (center frequency 75 Hz). Slepian

227 tapers result in more smoothing in the frequency domain and allowed us to reconstruct activity in a  
 228 wider frequency range. A common spatial filter was created for each frequency based on all trials.  
 229 This filter was consequently applied to congruent and incongruent trials separately. We computed  
 230 relative change in power for incongruent versus congruent (incongruent - congruent) / (incongruent  
 231 + congruent) to assess differences between conditions. Region labeling was done based on the  
 232 Harvard-Oxford atlas implemented in FSL (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>; RRID:SCR\_002823).

### 233 *Spatial filters applied to ROIs*

234 To assess whether gamma-band power is linked to theta-band phase we constructed three  
 235 spatial filters using linearly constrained minimum variance (LCMV) beamforming. Peak locations for  
 236 the phase-amplitude analyses were defined based on the peak grid-point resulting from the group  
 237 level brain-behavior correlation analysis for the theta-band [aPFC; MNI: 40 48 -6], and the group level  
 238 gamma-band congruency effect; left Postcentral Gyrus [-28 -32 64] and right Parietal Superior  
 239 Lobule/Postcentral Gyrus [28 -42 70]. These filters were applied to the MEG data after which the  
 240 dipole direction containing most variance was extracted.

### 241 *Brain-behavior correlations*

242 The source-reconstructed neural congruency-effects in theta- and beta-band power were  
 243 correlated with condition differences in reaction time (behavioral congruency-effect). We calculated  
 244 the correlation between the behavioral and the neural congruency-effects for each grid-point after  
 245 which we used Fisher's z transform to convert Spearman's *r* values into z values.

246 Trial-by-trial estimates [-0.5 s until response] of aPFC theta-band power were obtained from  
 247 aPFC peak grid-point resulting from the group brain-behavior correlation (centered at [40 48 -6]).  
 248 Trial-by-trial estimates of parieto-frontal beta-band power were obtained from a precentral grid-  
 249 point (centered at [50 -10 36]), resulting from the group level brain-behavior correlation. For each  
 250 subject, we set up a multiple regression model. First, we used trial-by-trial estimates of theta-band

251 power (aPFC), beta-band power (precentral), and their interaction ( $\text{theta}_{\text{aPFC}} * \text{beta}_{\text{precentral}}$ ) as  
 252 predictors of the timeseries of reaction times, separately for congruent and incongruent trials. The  
 253 regressors were z-scored within each condition, and regression parameters were estimated for each  
 254 condition and participant separately using robust regression (Matlab function *robustfit*).  
 255 Standardized beta values for each subject were used in a second-level analysis testing whether trial-  
 256 by-trial aPFC theta- and precentral beta-power better accounted for reaction time variance during  
 257 incongruent than during congruent trials (one-sided dependent-sample t-tests in SPSS, IBM SPSS  
 258 statistics; RRID:SCR\_002865), and whether those regression effects were different from zero (one  
 259 sample t-tests). In this approach single-trial estimates of power are regressed against single-trial  
 260 reaction times separately for each condition, a procedure that is orthogonal to the group-level  
 261 correlation between behavioral-congruency and congruency in theta- and beta-band power.

#### 262 *Connectivity analysis*

263 To assess whether aPFC influences downstream areas by influencing beta-band activity we  
 264 correlated condition differences in theta-band power extracted from aPFC [MNI: 40 48 -6] with  
 265 whole brain condition differences in beta-band power. Spearman's  $r$  values were transformed to  $z$   
 266 values using Fisher's transform.

267 For theta-gamma coupling we decomposed a spatial filter applied to the aPFC [MNI: 40 48 -6]  
 268 into 6 Hz complex signal using STFFT with a 500 ms window tapered with a Hanning filter, moving in  
 269 steps of 1 ms, after which the peak times between -0.5 s and response were extracted. Next, we  
 270 time-locked the remaining reconstructed time series (which were extracted from peak locations in  
 271 the gamma-band condition difference) around each theta-band peak time point. From this (theta  
 272 peak-locked) signal we extracted gamma-band [40 – 130 Hz] power by performing STFFT tapered  
 273 with a Hanning window containing 6 cycles per frequency band ( $dT = 6 / f$ ) and moving in steps of 10  
 274 ms. We computed relative change in TFR between conditions for the phase-locked gamma-band  
 275 power. We tested whether the gamma-band condition difference changed as a function of the phase

276 of the theta-band extracted from aPFC, an approach which is orthogonal to testing for a difference  
 277 between the experimental conditions. For interpretational purposes, we also computed the event  
 278 related field (ERF) of the phase-locked signal from the aPFC to show the underlying theta-band  
 279 waveform shape.

## 280 *Statistical analyses*

281 Statistical analyses on the sensor and source level consisted of cluster-based nonparametric  
 282 permutation tests (Maris and Oostenveld, 2007). This procedure ensures correction for multiple  
 283 comparisons over time, sensors (or grid points) and frequencies whilst also taking into account the  
 284 dependency in the data by clustering neighboring points showing the same effect. As test statistics  
 285 we used t-values on the sensor level data, z-values (fisher transformed  $r$  values) for brain behavior  
 286 correlations and theta-beta connectivity, and relative change (incongruent - congruent) / (congruent  
 287 + incongruent) for the theta-gamma coupling. Unless stated otherwise, the reported p-values refer to  
 288 cluster-corrected statistics.

## 289 **Results**

### 290 *Behavioral costs of control over social-emotional action*

291 Reaction times were longer for incongruent ( $M = 722$  ms,  $sd = 176$ ) as compared to  
 292 congruent trials ( $M = 680$  ms,  $sd = 147$ ) [ $t(39) = -4.33$ ,  $p < .001$ , figure 1B; effect size  $d = .26$ , calculated  
 293 as  $(M1-M2) / sd_{pooled}$ ]. In addition, we found higher accuracy levels for affect-congruent ( $M = 95.4\%$ ,  
 294  $sd = 4$ ) versus incongruent trials ( $M = 92.3\%$ ,  $sd = 6.5$ ) [ $t(39) = 3.07$ ,  $p = .004$ ,  $d = .57$ ]. These results  
 295 illustrate that the task is effective in inducing behavioral costs when participants need to override  
 296 their emotional action tendencies.

297 {Insert figure 1}

298

299 *aPFC theta-band power increases during emotional-action control*

300 As detailed in the Introduction, we hypothesized that frontal theta-band activity would be  
 301 involved in control over social-emotional action tendencies. We found stronger theta-band power  
 302 over anterior sensors before response, during control of automatic emotional actions (i.e.  
 303 incongruent vs congruent trials; center-frequency: 6 Hz, figure 2A, B). This congruency-effect effect is  
 304 statistically significant between 350 ms and 100 ms (maximum difference at 200 ms) before response  
 305 initiation, when controlling for multiple comparisons over sensors ( $N = 66$ ; ROI on all anterior  
 306 channels) and time points,  $p = .016$ ; figure 2A, C. Reconstructing the source locations of this  
 307 difference showed increases of theta-band activity for incongruent trials with local maxima at right  
 308 Frontal Pole (aPFC)/Superior Frontal Gyrus [20 40 50], Frontal Pole [26 70 8] and Frontal Orbital  
 309 Cortex [12 24 -24], figure 2D, with strongest theta-band increases in before response ([20 40 50];  
 310 figure 2E).

311 To localize theta-band activity that is relevant for behavior, we correlated condition  
 312 differences in theta-band power -0.5 s before- until response in each grid-point with reaction time  
 313 effects, over participants. ROI analysis on all frontal areas yielded a cluster of activity where the  
 314 theta-band congruency-effect correlated positively with reaction time congruency-effect (figure 2F,  
 315 G),  $r_{(38)} = .52$ ,  $p = .0007$  at peak grid point and  $r_{(38)} = .44$ ,  $p = .045$  for the whole cluster, corrected for  
 316 multiple comparisons over grid points. This cluster had two local maxima, at MNI coordinates [40 48 -  
 317 6] and [28 30 40], which correspond to right Frontal Pole and Middle Frontal Gyrus/Superior Frontal  
 318 Gyrus, respectively. This result indicates that those participants that show greater affect-  
 319 incongruity (as indexed by increased reaction-times for incongruent versus congruent trials) also  
 320 engage aPFC more strongly. Contralateral (left) Frontal Pole/Inferior Frontal Gyrus showed similar  
 321 correlations (maximum at [-34 36 12]) but this cluster remained below cluster-correction threshold.  
 322 No clusters survived whole-brain thresholding.

332 {Insert figure 2}

333

334 *Parietal and frontal beta-band activity decreases during emotional-action control*

Next, we tested whether increase in theta-band power would be accompanied by parietal beta-band desynchronization. A large cluster of decreased alpha/beta-band power in incongruent versus congruent condition resulted from the whole brain sensor-level analysis (figure 3A, B), with significant condition differences between 600 ms before response until response onset (maximum difference at time 0),  $p = .0064$  (figure 3C), corrected for multiple comparisons over time points, sensors ( $N=263$ ) and frequencies. Differences were present over most sensors (figure 3B) and ranged from 8 to 26 Hz (figure 3A), with a peak between 12 and 18 Hz. Splitting the observed effect in alpha (8-12 Hz) and beta-band (14-26 Hz; (e.g. De Lange et al., (2008)) showed a significant decrease for beta-band activity [14-26 Hz],  $p = .0023$ ; [-600 until response], but not for alpha-band [8-12 Hz,  $p = .11$ ]. For source reconstruction of the beta-band activity, we used 18 Hz as center frequency with a frequency smoothing of 4 Hz (giving 14-22 Hz) (De Lange et al., 2008; Jenkinson and Brown, 2011; Brinkman et al., 2014). Reconstructing beta-band activity revealed condition differences (i.e. stronger beta-band desynchronization in the incongruent condition) with a maximum in the right Superior



348 Parietal Lobule/Supramarginal Gyrus [44 -40 56], figure 3D. Time series reconstruction from right  
 349 Superior Parietal lobule (figure 3E) illustrates the beta-band desynchronization in this area peaks just  
 350 before response, and suggest a tight temporal relation with the frontal theta-band effect. These  
 351 results, combined with the aforementioned theta-band results indicate the involvement of aPFC  
 352 theta-band and PPC beta-band activity during the control over social-emotional action tendencies, in  
 353 close anatomical correspondence with previous studies on the control over emotional behavior (e.g.  
 354 Volman et al., 2011a, 2013).

355 Correlating beta-band power and behavioral congruency differences revealed a large cluster  
 356 with  $r_{(38)} = -.68$ ,  $p < .0001$  (peak grid point) and  $r_{(38)} = -.48$ ,  $p < .0001$  (whole cluster), over right  
 357 Precentral/Postcentral Gyrus with local maximum at [48 -2 36]; figure 3F. This correlation indicates  
 358 that participants with a large behavioral congruency effect show larger suppression in beta-band  
 359 power; figure 3G. Single trial beta-band power extracted from the peak location [48 -2 36] was  
 360 significantly correlated with behavioral performance,  $t_{(39)} = -3.06$ ,  $p = .002$  for incongruent, but not  
 361 for congruent trials;  $t_{(39)} = -.137$ ,  $p = .45$ , and also differed significantly between conditions;  $t_{(39)} = 1.8$ ,  
 362  $p = .04$ . This indicates that beta-band desynchronization over parieto-frontal regions is behaviorally  
 363 relevant when control over social-emotional actions is implemented.

364

365 {Insert figure 3}

366

367 *Effective connectivity between aPFC and parieto-frontal areas during emotional-action control*

368 As a next step, we tested whether aPFC theta-band activity modulates rhythms involved in  
 369 action selection. To assess connectivity between aPFC theta-band power and activity in anatomically  
 370 downstream areas, we correlated the condition difference in aPFC theta-band power (MNI: [40 48 -  
 371 6], local maximum of brain-behavior congruency effects, figure 2F,G) with the condition difference in

372 beta-band power across each brain grid point, on a subject-by-subject basis. Whole brain analysis  
 373 yielded a significant cluster,  $r_{(38)} = -.61$ ,  $p < .0001$  (peak grid point),  $r_{(38)} = -.46$ ,  $p = .021$  (whole cluster;  
 374 corrected for multiple comparisons over grid points) over right Precentral Gyrus/Postcentral Gyrus  
 375 with a local maximum at [50 -10 36], extending anteriorly into the Middle Frontal Gyrus and  
 376 posteriorly into the Superior Parietal Lobule (figure 4A; B). Contralateral (left) Precentral  
 377 Gyrus/Postcentral Gyrus showed similar connectivity below whole-brain corrected threshold. This  
 378 effect indicates that participants with larger increases in aPFC theta-band power during control over  
 379 social-emotional actions, also show a larger decrease in beta-band power over parieto-frontal areas.  
 380 These findings suggest functional coupling between those two oscillatory phenomena in those two  
 381 cortical regions. There were no significant connectivity effects following i) ROI analysis over the  
 382 parietal cortex, based on Volman 2011a; ii) exploratory correlational analyses with (theta-band) seed  
 383 grid point at [28 30 40] (Middle Frontal Gyrus/Superior Frontal Gyrus); iii) single trial correlations  
 384 between aPFC theta-band and beta-band activity from the connectivity peak location [50 -10 36]; or  
 385 iv) exploratory phase-amplitude coupling between aPFC theta-band phase and precentral beta-band  
 386 power.

387 {Insert figure 4}

388

389 *Gamma-band activity increases during emotional-action control*

390 Given that aPFC theta-band is thought to provide temporal organization to gamma-band  
 391 activity (Lisman and Jensen, 2013; Voytek et al., 2015), we explored whether controlling emotional  
 392 action tendencies resulted in changes in gamma-band power. To determine the frequency range of  
 393 gamma-band activity evoked in these experimental settings, we first compared gamma-band power  
 394 evoked before response with gamma-band power during baseline, over all trials. This comparison  
 395 showed an increase in power between 60 and 90 Hz (mid-gamma range; Buzsáki and Wang, (2012)),  
 396 localized over central sensors,  $p = .027$  corrected for multiple comparisons over frequencies, time

points and sensors (N=263). Comparing 60-90 Hz gamma-band power between conditions showed stronger power for incongruent than congruent trials over central sensors (figure 5A, B), starting 350 ms before response until 50 ms before response,  $p = .03$  (figure 5C), corrected for multiple comparisons for time points and sensors (N=263). Source reconstruction of gamma-band condition differences showed power increases with local maxima in right Parietal Superior Lobule/Postcentral Gyrus [28 -40 72], left Postcentral Gyrus [-28 -32 64] and left Superior Frontal Gyrus [-12 16 64] (figure 5D), indicating increased engagement of sensorimotor and parietal areas during control over prepotent habitual actions (figure 5E). There was no significant correlation between gamma-band congruency and reaction time congruency effects,  $r_{(38)} = .26$ ,  $p = .097$ .

Finally, to explore whether aPFC control over automatic action tendencies may involve coupling to sensorimotor gamma-oscillations, we explored the presence of phase-amplitude coupling between theta-band phase at aPFC [40 48 -6], and gamma-band power over left Central Sulcus [-28 -32 64] and right Parietal Superior Lobule/Postcentral Gyrus [28 -42 70]. In the incongruent condition, there was stronger gamma-band power over left Postcentral Gyrus during peaks- but not during troughs of the aPFC theta-band signal;  $p = .013$ ,  $p = .015$ , and  $p = .025$  for the first, second, and third cluster shown in figure 5F (left to right; corrected for multiple comparisons over time points and frequencies). These results indicate that the increased gamma-band power evoked over contralateral sensorimotor cortex during the control of prepotent habitual actions might be guided by long-range communication between aPFC and those sensorimotor areas.

{Insert figure 5}

## Discussion

This study explores neurophysiological mechanisms implementing control over social-emotional behavior. We show that the known contributions of aPFC and PPC to the control of social-emotional behavior are implemented through modulations of neural rhythmic activity in the theta-, beta-, and

422 gamma-band. More precisely, when participants select an affect-incongruent response to emotional  
 423 faces, theta-band power increases over aPFC. The increase in theta-band power corresponds to  
 424 decreases in beta-band power over parieto-frontal cortex, and theta phase-locked increases in  
 425 gamma-band power over sensorimotor areas. Those modulations of neural rhythmic activity, as well  
 426 as their temporal dynamics, are behaviorally relevant for the control of social-emotional behavior,  
 427 both between- as well as within-subjects. Trial-by-trial increases in reaction times during incongruent  
 428 trials are accounted for by increases in theta-band power over aPFC, and decreases in beta-band  
 429 power over parieto-frontal cortex.

#### 430 **Prefrontal theta-band oscillations during control of social-emotional behavior**

431 Previous work has shown the importance of theta-band oscillations in overcoming  
 432 motivational action biases in favor of goal-directed behavior (Cavanagh et al., 2013). Those theta-  
 433 band oscillations, evoked in the context of a pavlovian learning paradigm, emerged from the medial  
 434 prefrontal cortex (mPFC), a region frequently associated with cognitive control involving action  
 435 inhibition (Ridderinkhof et al., 2004) and conflict monitoring (Etkin et al., 2006, 2011). Here, we add  
 436 two novel elements to that knowledge. First, we show that the theta-band rhythm is also involved in  
 437 the proactive control of social-emotional action tendencies requiring the rapid selection of actions  
 438 alternative to a prepotent habitual response. This instance of cognitive control operates on the  
 439 interaction between emotional percepts and action selection, over and above the emotional value of  
 440 the stimulus or the emotional value of the response alone. Second, the theta-band rhythm  
 441 supporting this type of cognitive control emerges from the anterior-lateral prefrontal cortex.

442 The increased theta-band power observed in this study could be an instance of low-  
 443 frequency modulations of cortical ensembles (Jensen and Mazaheri, 2010), e.g. the frequently  
 444 observed theta-based coordination of medio-frontal neuronal ensembles during rule-retrieval  
 445 (Colgin, 2013; Harris and Gordon, 2015). However, the anatomical location and functional  
 446 characteristics of the theta-band effect suggest a more specific mechanism. Namely, we show that

447 this theta-band related form of control emerged before response delivery from the aPFC, rather than  
 448 during feedback-processing from medial frontal sources previously associated with inhibitory control  
 449 and memory retrieval (Cavanagh et al., 2011; Colgin, 2013; Cavanagh and Frank, 2014). The aPFC,  
 450 consistently involved in previous fMRI and transcranial magnetic stimulation studies of social-  
 451 emotional action-control (Kalisch, 2009; Volman et al., 2011a, 2013; Morawetz et al., 2017), has been  
 452 associated with the ability to control immediate action tendencies while implementing more abstract  
 453 goals (Burgess et al., 2007; Badre and D'Esposito, 2009; Koechlin, 2016; Mansouri et al., 2017),  
 454 possibly by keeping online non-chosen response options (Boorman et al., 2009). Controlling  
 455 emotional-action tendencies, differently from emotional Stroop-like tasks involving stimulus-level  
 456 conflict, requires considering the relative benefit of the unchosen behavioral strategy, before a  
 457 switch in response set is implemented (Boorman et al., 2009). The timing, anatomical location, and  
 458 downstream effects of the current theta-band findings fit with the notion that control of emotional  
 459 action tendencies involves maintenance of counterfactual choices in aPFC.

#### 460 **Parieto-frontal beta-band oscillations during control of social-emotional behavior**

461 Emotional control evoked beta-band desynchronization, localized to parietal cortex. Those  
 462 features are not compatible with the beta-band synchronization elicited in inferior frontal gyrus (IFG)  
 463 during action inhibition (Swann et al., 2012; Aron et al., 2014; Bastin et al., 2014; Picazio et al., 2014).  
 464 Here, beta-band desynchronization likely reflects increased engagement of areas involved in action  
 465 selection (Brinkman et al., 2014) through release from tonic cortical inhibition (Khanna and Carmena,  
 466 2017) and increased cortico-spinal excitability (van Elswijk et al., 2010). This release from inhibition is  
 467 facilitated by decreases in GABA-ergic tone (Jensen et al., 2005; Yamawaki et al., 2008) and  
 468 accompanied by increased gamma-band and spiking activity (Spinks et al., 2008; Donner et al., 2009).  
 469 The parieto-frontal reduction in beta-band power we observe is inversely proportional to trial-by-  
 470 trial slowing of responses during incongruent trials, and significantly more so than during congruent  
 471 trials, suggesting that this effect is not a trivial consequence of participants preparing a generic

472 motor response, nor a systematic effect of task difficulty. In fact, the enhanced tonic beta-band  
 473 desynchronization observed during incongruent trials might reflect stronger disinhibition of parieto-  
 474 frontal circuits when competition between multiple possible actions needs to be resolved and a  
 475 larger neuronal search space needs to be considered (Cisek and Kalaska, 2010; Grent et al., 2013;  
 476 Brinkman et al., 2014).

#### 477 **Sensorimotor gamma-band oscillations during control over social-emotional behavior**

478 Gamma-band synchronization in the motor system is linked to action preparation and  
 479 movement selection (Donner et al., 2009; Schoffelen et al., 2011). When multiple response options  
 480 are available during action preparation, such as during response conflict, increases in gamma-band  
 481 oscillations are observed. This is often interpreted as simultaneous activation of multiple active  
 482 response-sets (Gaetz et al., 2013; Grent et al., 2013), with an automatically triggered action  
 483 competing with an alternative rule-based action. The increase in gamma-band power we observe in  
 484 the affect-incongruent condition might reflect enhanced coordination of local neuronal ensembles  
 485 (Buzsáki and Wang, 2012) towards a state space suitable to initiate the correct, rule-based action (De  
 486 Lange et al., 2008; Churchland et al., 2010; Kaufman et al., 2014), and away from the prepotent  
 487 habitual action state. The phasic temporal relation between increases in central gamma-band power  
 488 and peaks in aPFC theta-band oscillations indicates that selection of an alternative action could be  
 489 implemented through inter-regional communication via phase-dependent modulations of gamma-  
 490 band rhythms (Lisman and Jensen, 2013; Voytek et al., 2015)

#### 491 **Interpretational issues**

492 It remains to be seen whether the relation between theta-band effects in aPFC, and  
 493 downstream beta- and gamma-band effects, constitutes a functionally directional and mono-synaptic  
 494 interaction. It is known that aPFC sits at the top of the prefrontal hierarchy and projects to parietal  
 495 and premotor areas (Ramnani and Owen, 2004; Miller and D'Esposito, 2005; Voytek et al., 2015;  
 496 Koechlin, 2016) and the timing of our effects suggests that aPFC might provide top-down regulation.

497 However, given the lack of precise knowledge on the feedforward versus feedback connectivity of  
 498 this circuit in humans (Neubert et al., 2014), the directionality of these effects remains elusive. The  
 499 current findings do not exclude that other regions involved in emotional action selection could  
 500 mediate inter-regional couplings between aPFC and parieto-frontal cortex, such as the pulvinar  
 501 (Tyborowska et al., 2016), or the amygdala. The latter has been shown to be down-regulated by aPFC  
 502 during social-emotional control (Volman et al., 2013), and it is directly influenced by frontal theta-  
 503 band oscillations during freezing (Karalis et al., 2016).

504 It could be argued that the theta-band effects we report are generic by-products of increased  
 505 anxiety during incongruent trials. Previous studies have shown that theta-band activity in mPFC is  
 506 involved in anxiety and fear behavior (Cavanagh and Shackman, 2015; Harris and Gordon, 2015), with  
 507 increased theta-band connectivity between hippocampus and mPFC during fear-related inhibition of  
 508 behavior (Adhikari et al., 2010; Khemka et al., 2017) and increased theta-band activity over mPFC in  
 509 anxious individuals (Cavanagh and Shackman, 2015). However, the current changes in theta-band  
 510 power were modulated by variations in performance on a trial-by-trial basis, an effect orthogonal to  
 511 the systematic changes possibly related to state anxiety.

512 Source-level changes in aPFC theta-band and fronto-parietal beta-band power arise in the  
 513 right hemisphere. However, inspection of the data shows sub-threshold effects in the corresponding  
 514 contralateral regions, suggesting that the right-hemispheric lateralization is a threshold effect of a  
 515 bilateral process, in line with previous fMRI reports (Volman et al., 2011b, 2013) and with the sensor-  
 516 level scalp topographies.

517 The anterior frontal location of the theta-band effect could be an artifact driven by task-  
 518 related changes in head or eye position. This potential source of between-conditions differences is  
 519 unlikely to account for the findings. There were identical stimuli and movements across conditions,  
 520 head movements were monitored with millimeter precision during task performance (Stolk et al.,  
 521 2013), and ocular artifacts were aggressively removed with ICA.

Phase-amplitude couplings can be inflated by non-sinusoidal oscillations (Lozano-Soldevilla et al., 2016; Cole et al., 2017), sharp transients in the data (Aru et al., 2015), or harmonics of lower frequencies (Jensen et al., 2016). In our case, theta-related harmonics and sharp transients are unlikely to play a role, given that the theta-band and gamma-band signals originate from different cortical regions, with a clear sinusoidal theta-band signal in aPFC. Stronger theta-band power during incongruent trials might lead to more robust phase estimation, but this does not invalidate the presence of increased gamma-band power during peaks of the theta-band oscillation in aPFC.

## Conclusion

This study defines neural responses to the problem of controlling human social-emotional behavior. Participants implement rapid changes in their predominant response set and select an alternative course of action by increasing theta-band power over aPFC, tonically decreasing beta-band power over parieto-frontal cortex, and transiently increasing gamma-band power over parietal and sensorimotor cortex through a mechanism phase-locked to prefrontal theta oscillations. These findings provide clear mechanistic targets for interventional studies aimed at enhancing control over social-emotional behaviors in a number of psychopathologies.

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718

# 719 Figure Legends

720

## 721 Figure 1: *Approach-avoidance (AA) task and behavioral results.*

722 *Panel A shows a schematic representation of the affect-congruent and affect-incongruent conditions*  
 723 *in the AA task. Panel B shows average reaction times for each participant (N=40) and condition.*  
 724 *Responses are slower during incongruent trials. \*:  $t_{(39)} = -4.33$ ,  $p < .001$ .*

725

726 **Figure 2: *Emotional control increases theta-band power in anterior prefrontal cortex.*** A) time-  
 727 frequency plot of between conditions power differences (congruency effect: incongruent – congruent  
 728 / congruent + incongruent) averaged over sensors with a significant effect (see panel B). Time 0:  
 729 response onset. The dashed box shows the time-frequency interval with a significant congruency  
 730 effect [-350 to -100 ms before response; 6 Hz]. B) topographic distribution of sensors with a  
 731 significant congruency effect at 6 Hz (marked by stars). C) changes over time in theta-band power (6  
 732 Hz) averaged across significant sensors (see panel B). The epoch with a significant difference between  
 733 conditions is marked in grey. D) Cortical distribution of theta-band congruency effects. E) Time series  
 734 of 6 Hz activity extracted from right frontal pole/ superior frontal gyrus [20 40 50]. F) Cortical

735 distribution of correlations between theta-band and behavioral congruency effects, with a significant  
 736 cluster over aPFC (dashed black circle, MNI coordinates of local maximum: [40 48 -6]). G) correlation  
 737 between theta-band and behavioral congruency effects. Black dots represent measurements from  
 738 each participant. Theta-band power changes are extracted from the local maximum in aPFC.

739

740 **Figure 3: Emotional control decreases beta-band power in parietal and frontal cortex.** A) time-  
 741 frequency plot of between conditions power differences (congruency effect: incongruent – congruent  
 742 / congruent + incongruent) averaged over sensors with a significant effect (see panel B). Time 0:  
 743 response onset. The dashed box shows the time-frequency interval with a significant congruency  
 744 effect [-600 to 0 ms before response; 14-26 Hz]. B) topographic distribution of sensors with a  
 745 significant congruency effect at 14-26 Hz (marked by stars). C) changes over time in beta-band power  
 746 (14-26 Hz) averaged across significant sensors (see panel B). The epoch with a significant difference  
 747 between conditions is marked in grey. D) Cortical distribution of beta-band congruency effects (center  
 748 frequency 18 Hz). E) Time series of 18 Hz activity extracted from Superior Parietal Lobule [44 -40 56].  
 749 F) Cortical distribution of correlations between beta-band (18 Hz) and behavioral congruency effects,  
 750 with a significant cluster over right precentral gyrus (MNI coordinates of local maximum: [48 -2 36]).  
 751 G) correlation between beta-band and behavioral congruency effects. Black dots represent  
 752 measurements from each participant. Beta-band power changes are extracted from the right  
 753 precentral maximum.

754

755 **Figure 4: Emotional control increases connectivity between aPFC and fronto-parietal areas.** A)  
 756 Cortical distribution (uncorrected for multiple comparisons) of correlations between beta-band  
 757 congruency effects and theta-band congruency effects extracted from aPFC (in red, from Figure 2E).  
 758 The cluster over the right precentral gyrus (MNI coordinates of local maximum: [50 -10 36]) is  
 759 significant. B) correlation between aPFC theta-band and precentral beta-band congruency effects.

760 Black dots represent measurements from each participant. Beta-band power changes are extracted  
 761 from the right precentral maximum.

762

763 **Figure 5: Emotional control increases gamma-band power in parietal and frontal cortex during**  
 764 **peaks of theta-band oscillations in aPFC.** A) Time-frequency plot of between conditions power  
 765 differences (congruency effect: incongruent – congruent / congruent + incongruent) averaged over  
 766 sensors with a significant effect (see panel B). Time 0: response onset. The dashed box shows the  
 767 time-frequency interval with a significant congruency effect [-350 to -50 ms before response; 60-90  
 768 Hz]. B) topographic distribution of sensors with a significant congruency effect at 60-90 Hz (marked  
 769 by stars). C) changes over time in gamma-band power (60-90 Hz) averaged across significant sensors  
 770 (see panel B). D) Cortical distribution of relative gamma-band congruency effects, with a significant  
 771 cluster around the left central sulcus [-28 -32 64]. E) Time series of 60-90 Hz activity extracted from  
 772 left central sulcus [-28 -32 64]. F) Time-frequency plot of gamma-band power congruency effects  
 773 extracted from the local maximum in the left central sulcus (panel F); phase-locked to the aPFC theta-  
 774 band signal before response. Contours are drawn around significant clusters where power is stronger  
 775 in incongruent versus congruent trials. G) event related field of the theta-band signal extracted from  
 776 aPFC.

777













