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Abstract

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

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

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

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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Introduction

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

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

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

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

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

Materials and Methods

Participants

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

Materials and apparatus

The task was programmed using Presentation software version 16.4 (neurobs.com; RRID:SCR_002521). Stimuli were presented using a PROPixx beamer with a refresh rate of 120 Hz and a resolution of 1920:1080. MEG was acquired using a whole brain CTF-275 system with axial gradiometers. Data were sampled at 1200 Hz after a 300 Hz lowpass filter was applied. Four sensors (MLF62, MLC32, MLC11 & MRF66) were permanently disabled due to high noise. The helmet was set at 15° and the participants were seated 80 cm from the screen. Head location was measured using localization coils in both ear canals and on the nasion and was continuously monitored using online head localization software (Stolk et al., 2013). In case of large deviations from the initial head position (+5 mm) we paused the experiment and instructed the subject to move back to the original position. During the task, participants responded using a customized Fiber Optic Joystick (fORP design), that was calibrated for each participant prior to the experiment. A displacement of 20% 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 ($theta_{aPFC}$*$beta_{precentral}$) 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

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

Statistical analyses

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

Results

Behavioral costs of control over social-emotional action

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

{Insert figure 1}

aPFC theta-band power increases during emotional-action control

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

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

Next, we implemented a post-hoc exploratory analysis to examine whether the relation between increased theta-band power and emotional action control holds even on a trial-by-trial basis. Comparing single trial theta-band power derived from aPFC (MNI: [40 48 -6]) using one-sided t-tests confirmed significant differences between conditions for theta-band power: $t_{(39)} = -1.77$, $p = .043$. Theta-band power in the incongruent condition significantly correlated with behavioral performance in the same condition, $t_{(39)} = 2.69$, p = .005. This was not the case for the congruent condition $t_{(39)} = -.29$, p = .77. Together these results confirm our hypothesis that theta-band power is a positive predictor of reaction time and show that aPFC is recruited more strongly with increased incongruence, on a subject-by-subject as well as on a trial-by-trial basis.

{Insert figure 2}

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

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

{Insert figure 4}

Gamma-band activity increases during emotional-action control

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

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

406 Finally, to explore whether aPFC control over automatic action tenedencies may involve
407 coupling to sensorimotor gamma-oscillations, we explored the presence of phase-amplitude coupling
408 between theta-band phase at aPFC [40 48 -6], and gamma-band power over left Central Sulcus [-28 -
409 32 64] and right Parietal Superior Lobule/Postcentral Gyrus [28 -42 70]. In the incongruent condition,
410 there was stronger gamma-band power over left Postcentral Gyrus during peaks- but not during
411 throughs of the aPFC theta-band signal; p = .013, p = .015, and p = .025 for the first, second, and third
412 cluster shown in figure 5F (left to right; corrected for multiple comparisons over time points and
413 frequencies). These results indicate that the increased gamma-band power evoked over controlateral
414 sensorimotor cortex during the control of prepotent habitual actions might be guided by long-range
415 communication between aPFC and those sensorimotor areas.

416 **{Insert figure 5}**

417

418 **Discussion**

419 This study explores neurophysiological mechanisms implementing control over social-emotional
420 behavior. We show that the known contributions of aPFC and PPC to the control of social-emotional
421 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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Figure Legends

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

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

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

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

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

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

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

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