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Why don't you like me? Midfrontal theta power in response to unexpected peer rejection feedback

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Abstract

Social connectedness theory posits that the brain processes social rejection as a threat to survival. Recent electrophysiological evidence suggests that midfrontal theta (4-8 Hz) oscillations in the EEG provide a window on the processing of social rejection. Here we examined midfrontal theta dynamics (power and inter-trial phase synchrony) during the processing of social evaluative feedback. We employed the Social Judgment paradigm in which 56 undergraduate women (mean age = 19.67 years) were asked to communicate their expectancies about being liked vs. disliked by unknown peers. Expectancies were followed by feedback indicating social acceptance vs. rejection. Results revealed a significant increase in EEG theta power to unexpected social rejection feedback. This EEG theta response could be source-localized to brain regions typically reported during activation of the saliency network (i.e., dorsal anterior cingulate cortex, insula, inferior frontal gyrus, frontal pole, and the supplementary motor area). Theta phase dynamics mimicked the behavior of the time-domain averaged feedback-related negativity (FRN) by showing stronger phase synchrony for feedback that was unexpected vs. expected. Theta phase, however, differed from the FRN by also displaying stronger phase synchrony in response to rejection vs. acceptance feedback. Together, this study highlights distinct roles for midfrontal theta power and phase synchrony in response to social evaluative feedback. Our findings contribute to the literature by showing that midfrontal theta oscillatory power is sensitive to social rejection but only when peer rejection is unexpected, and this theta response is governed by a widely distributed neural network implicated in saliency detection and conflict monitoring.

Keywords: EEG, feedback, phase synchrony, social rejection, source localization, theta power

Introduction

From an evolutionary perspective, people are strongly motivated to gain social acceptance as social disconnection may diminish fundamental resources for survival (Baumeister & Leary, 1995). It has been hypothesized that people have evolved a highly sensitive threat-detection system that could protect them from social disconnection (Eisenberger & Lieberman, 2004), and dysfunction of this system has been linked to a wide range of psychological disorders (e.g., from diminished self-esteem to social anxiety and depression) (Masten et al., 2011; Masten et al., 2009; Nishiyama et al., 2015; Somerville, Kelley, & Heatherton, 2010). Neuroimaging studies have indeed shown that the brain is equipped with an efficient alarm system that quickly detects signs of social disconnection (Eisenberger, 2012). Two core structures of this neural alarm system are the anterior cingulate cortex (ACC) and the anterior insula (AI), and recently it has been shown that increases in AI generated theta (4-8 Hz) oscillatory power can be observed during social exclusion events (Cristofori et al., 2013). Notably, oscillatory activity in the theta band is also involved in the processing of negative feedback (e.g., Van de Vijver, Ridderinkhof, & Cohen, 2011), but typically these studies investigate performance monitoring in which the increase in theta power after negative performance feedback is interpreted to reflect a prediction error of the participant. The question thus remains whether theta oscillatory reactivity can be taken to reflect as a neural signature of social isolation, especially since the neural substrates that generate rhythmic activity in the theta band are associated with a variety of cognitive affective processes, including both negative affect and cognitive control (Shackman et al., 2011).

The majority of studies investigating the neural correlates of the emotional distress resulting from social disconnection have used a paradigm coined ‘Cyberball’ (Eisenberger, Lieberman, & Williams, 2003), a virtual ball-tossing game in which participants are first included and then excluded. Using Cyberball, fMRI studies have found increased activation in both dorsal and ventral parts of the ACC, with the ventral ACC being most sensitive to the experience of social exclusion (Eisenberger & Lieberman, 2004). Additionally, event-related brain potential (ERP) studies typically show that exclusion in Cyberball is manifested by a late positive potential (LPP) (Crowley, Wu, Molfese, & Mayes, 2010; Gutz, Kupper, Renneberg, & Niedeggen, 2011; Sreekrishnan et al., 2014). Recent EEG studies have shown that this LPP during social exclusion is governed by theta oscillatory activity (Cristofori et al., 2013; Van Noordt, White, Wu, Mayes, & Crowley, 2015), and this activity in theta band power was interpreted as a neural signature of 'social pain' (Cristofori et al., 2013). Although these Cyberball studies have contributed considerably to our understanding of the neural mechanisms of social pain processing, a notable limitation to the Cyberball paradigm is that the exclusion blocks elicit not only emotional distress due to social exclusion, but also cognitive conflict due to – for example – participants' expectancy violation about receiving the ball (cf., Somerville, Heatherton, & Kelley, 2006; Van der Veen, Van der Molen, Sahibdin, & Franken, 2014; Woo et al., 2014).

A paradigm that has been successfully used in dissociating cognitive conflict from the psychophysiological processes induced by a social threat is the Social Judgment paradigm (SJP), introduced by Somerville et al. (2006). In this paradigm, participants are led to believe that they have been evaluated based on first impressions by a panel of peers. During the experiment participants are asked to predict whether these peers liked or disliked the participant. Thereafter participants receive the actual peer feedback communicating social rejection or acceptance that is either congruent or incongruent with their prior predictions. The advantage of the SJP is that it allows for a detailed assessment of social acceptance vs. rejection processing vis-à-vis participants' expectancies about the social evaluative outcome.

In previous ERP studies, we examined the feedback-related negativity (FRN) elicited by social evaluative peer feedback in the SJP. The FRN is a frontocentral negative deflection in the ERP peaking approximately 250 ms after the onset of the feedback stimulus, and a vast literature suggests that the FRN is generated by the ACC (Bellebaum, Polezzi, & Daum, 2010; Segalowitz et al., 2010; Warren, Hyman, Seamans, & Holroyd, 2015). In terms of its functional significance, the FRN is typically interpreted to reflect prediction error (Alexander & Brown, 2011). That is, the FRN is larger in amplitude for feedback that is incongruent with individuals' prior expectancies about the feedback outcome. Although it has been frequently observed that the FRN is larger for feedback that is worse than expected (Gehring & Willoughby, 2002), our two previous ERP studies revealed that FRN was larger for unexpected vs. expected feedback in the SJP (Dekkers, Van der Molen, Gunther Moor, Van der Veen, & Van der Molen, 2015; Van der Molen et al., 2014). It should be acknowledged, however, that these ERP analyses did not capture all relevant information that is contained in the EEG. Due to single-trial averaging, the FRN represents the time-domain average of neural activity that is time-locked (phase-locked) to the onset of the feedback stimulus, and thus lacks information about neural activity that is not phase-locked with the event (Makeig, Debener, Onton, & Delorme, 2004). Myriad of studies demonstrated that non-phase locked oscillatory power yields cognitively relevant data, and specifically modulations in theta-band power have shown to be sensitive to feedback manipulations in various cognitive and affective studies (e.g., Cavanagh, Figueroa, Cohen, & Frank, 2012; Christie & Tata, 2009; Cohen, Elger, & Fell, 2009; Crowley et al., 2014; De Pascalis, Varriale, & Rotonda, 2012).

Here we will employ the SJP to investigate rhythmic changes in both theta-band oscillatory power (i.e., the magnitude of neural activation) and inter-trial phase synchrony (i.e., the consistency in timing of oscillatory activity) during social evaluative feedback processing. Our hypotheses were directed at the theta-band, since Cyberball studies have reported on increased theta power during social exclusion (Cristofori et al., 2013; Van Noordt et al., 2015), and prior ERP studies have linked the FRN to modulations in theta power and phase synchrony (Cavanagh, Frank, Klein, & Allen, 2010; Van de Vijver et al., 2011). We tested two competing hypotheses that should reveal whether theta power is specifically implicated in processing social rejection, or whether expectancy violation is contributing to the involvement of theta power in processing social rejection. If indeed theta power is a neural correlate of processing social rejection (Cristofori et al., 2013; Van Noordt et al., 2015), than theta power should be significantly increased in social rejection conditions, irrespective of participants' prior expectancies. However, if theta power is modulated by expectancy violation, a significant increase in theta power would be expected in conditions in which social evaluative feedback violates participants' prior predictions. Further, we exploratively examined source activity of feedback-related theta power and, based on prior studies (Cohen, 2014; Cristofori et al., 2013), expected to find the ACC and AI as main source generators of this EEG signal. With respect to theta phase synchrony, we hypothesized to find stronger inter-trial phase synchrony in conditions in which social evaluative feedback violated participants' expectancies. This hypothesis is in line with our previous FRN findings (Dekkers et al., 2015; Van der Molen et al., 2014) and is guided by the fact that the FRN reflects neural activity that is phase-locked to the feedback stimulus. To warrant similarity in results between the FRN and theta inter-trial phase synchrony in social evaluative feedback processing, we also measured the FRN component in the ERP.

Method

Participants

Seventy-one right-handed female undergraduate students participated in this study[1]. Fifteen participants were excluded from analysis due to recording problems (*n* = 5), bad EEG data (*n* = 9) or disbelief in the cover story of the SJP (*n* = 1), yielding a total sample of 56 participants

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[1] A sub-sample (*n*=31) of the current participants took part in a previous study examining EEG brain potential responses to feedback in the SJP (Van der Molen *et al.*, 2014).

for the analyses (age range = 18-24 years, *M* = 19.67, *SD* = 1.47). Participants were recruited from or within the proximity of Leiden University and received course credit or fixed payment for participation. Participants had normal or corrected to normal vision, were right-handed, and free from use of psychoactive medication. All participants signed informed consent prior to the experiment. The study's protocol was reviewed and approved by the medical ethical review committee of the Leiden University Medical Center.

Social Judgment paradigm

We employed a modified version of the SJP (Gunther Moor, Crone, & Van der Molen, 2010; Somerville et al., 2006; Van der Molen et al., 2014). Participants were led to believe that they were enrolled in a study on first impressions. Prior to testing, participants were required to send a personal portrait photograph to the investigators. A panel of peers from other universities would then evaluate this photograph. This peer panel would be asked to judge – based on their first impressions – whether they liked or disliked the participant. Approximately two weeks later, participants were invited to the lab for the EEG experiment. Prior to testing, participants were told that they would be viewing a portrait photograph of each member of the peer panel. Their task was to indicate whether they thought to be liked or disliked by the peer on the photograph. Subsequently, peer feedback was presented communicating social acceptance or rejection feedback that was either congruent or incongruent with the participants' expectancies. In reality, a peer panel never evaluated the participants' photographs, and fictitious peer feedback was pseudo-randomly presented by the computer. The combination of the participant's expectancy (expected social acceptance vs. expected social rejection) and feedback outcome (social acceptance vs. social rejection) generates four conditions: expected acceptance, expected rejection, unexpected acceptance and unexpected rejection.

A total of 160 photographs of peers were used (50% male), derived from taking photographs of undergraduates from different universities. These photos have been obtained in a prior study (Gunther Moor et al., 2010; Van der Molen et al., 2014). The photos were shown on a 17-inch monitor (60 Hz refresh rate; visual angle [width x height] = 4.66° x 6.05°) using E-prime 2.0 stimulus presentation software (Psychology Software Tools, Pittsburgh PA). All peer photographs had a neutral facial expression, as ascertained with the Self-Assessment Manikin (SAM; Bradley & Lang, 1994). A schematic of a trial sequence is presented in Figure 1. Each trial started with the presentation of the cue (i.e., photo of a peer) that remained on the screen during the remainder of the trial. Participants were required to indicate whether the peer liked or disliked the participant by pressing one of two buttons on an armrest, corresponding to expected social acceptance ("YES") or rejection ("NO"). Left versus right buttons to indicate expected social rejection versus acceptance were counterbalanced across participants. Participants were required to provide their expectancies within a 3000 ms response window that started with the onset of the cue. If participants did not respond within this time-window, the feedback "too slow" appeared on the screen, followed by a new trial. If participants did respond on time, the response window was terminated and participants' expectancies ("YES" or "NO") were immediately presented on the computer screen to the left of the peer's face. Peer feedback was presented after a fixed interval of 3000 ms, to the right of the peer's face, communicating social acceptance ("YES") or rejection ("NO"). On 50% of the trials, participants received social rejection feedback. Between trials, a fixation cross was presented in the middle of the screen for a jittered duration between 500-1500 ms. The experiment started with 10 practice trials, followed by three experimental blocks of 50 trials, and ended with filling out self-report questionnaires (not included in the present report) and the writing down of participants' experiences and thoughts about the experiment. Participants were debriefed about the experiment by letter, after the last participant was tested.

--- insert Figure 1 about here ---

Signal recording and processing

EEG data were acquired with a Biosemi Active Two system (Biosemi, Amsterdam, the Netherlands) at a 1024 Hz sampling rate from 64 active scalp electrodes placed in an electrode cap according to the 10/20 system. Vertical eye-movements were measured with two electrodes placed above and below the left eye; horizontal eye-movements measured from two electrodes placed at the left and right canthus. Two electrodes placed at the mastoids were used for offline reference. The common mode sense and driven right leg electrodes were used as online reference, which are part of a feedback loop to replace the conventional ground electrode.

Data were offline analyzed using Brain Vision Analyzer (BVA 2.0.4; Brain Products GmbH, Munich, Germany), down-sampled to 512 Hz, and re-referenced to the average of the left and right mastoid electrodes. After applying a 1-40 Hz band-pass filter (24 dB/oct) and a 50 Hz notch filter, time-series were epoched from -4 s to + 4 s surrounding the onset of the feedback. Epochs were visually screened for artifacts. Epochs containing artifacts other than eye blinks (e.g., muscular activity, clipping, and movement artifacts) were removed from the data, as well as were trials that contained invalid responses (e.g., responses outside the response window and/or multiple responses within the response window). Bad channels were corrected with spherical spline interpolation and eye blinks were automatically removed from the data with the Ocular Independent Component Analysis method, as implemented in BVA. Next, a Current Source Density (CSD) transformation was applied to the data. CSD transformation yields a reference-free spatially enhanced representation of the direction, location, and intensity of high-spatial-frequency activity (Kayser & Tenke, 2006; Tenke & Kayser, 2012), improving topographical localization and validity of phase-based synchronization analyses due to minimizing the effects of volume conduction (Tenke & Kayser, 2015). Table 1 shows the average number of artifact-free EEG segments per condition used for analysis.

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Time-frequency power analyses

Time-frequency characteristics were extracted from the EEG time series by convolution of the single trials with a family of complex Morlet wavelets, which can be defined as Gaussian-windowed sine waves, which increased from 1 to 40 Hz in 40 logarithmically spaced steps (wavelet length = 166.01 ms). The Morlet parameter was set to 5 to obtain an adequate trade-off between time and frequency precision. The unit energy normalization method as implemented in Brain Vision Analyzer was used. This method gives all frequency layers the same energy value of 1, which allows for comparison of the signal across frequencies layers. After convolution of the complex Morlet wavelet with the single trial data, time-frequency power was extracted from the complex signal and was normalized using a ratio-change from the -500 to -200 ms pre-stimulus baseline. By collapsing over the four conditions we observed a pronounced burst in power at Fz and FCz for theta power during a 300-500 ms post-feedback time-window. We used data from these frontal midline electrodes obtained during this time-window for further analysis.

Source localization analyses

Source-localization of feedback-related theta power was performed on the single EEG trials per feedback condition using Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011), a Matlab software package freely available and documented online (http://neuroimage.usc.edu/brainstorm). Since the calculation of the inverse solution – and the resulting current density estimations of source activity – assumes that EEG is referenced according to an average reference montage, we performed an average reference on the raw, artifact-free, and baseline corrected single trials prior to source-localization. Due to the absence of individual MRI anatomies of the participants, we used the default anatomy of the standard MNI brain (Colin27) as a tessellated cortical mesh template surface. The default Biosemi 64 channel layout was co-registered with the MRI anatomy and electrodes were projected to the scalp surface. OpenMEEG software (Gramfort, Papadopoulo, Olivi, & Clerc, 2010) – as implemented in Brainstorm – was used to calculate a symmetric boundary element model as an EEG forward model of volume currents (the adaptive integration method with default settings was applied). This is a volume conduction method that employs three realistic layers that correspond to the head surface (1922 vertices, relative scalp conductivity = 1), the outer skull (1922 vertices, relative skull conductivity = .0125), and the inner skull (1922 vertices, relative brain conductivity = 1) (Ambrosini & Vallesi, 2016). Prior to source-localization, a noise covariance matrix was calculated based on data from the pre-trial baseline (-500 to -200 ms) to estimate the level of noise at the electrodes. Subsequently, cortically unconstrained source-localization was performed on the EEG single-trials using the depth-weighted minimum norm estimate (wMNE) algorithm (Lin et al., 2006) over a set of 3 x 5005 elementary current dipoles distributed over the cortical envelope. Although the source estimation is limited by the absence of individual MRI anatomies, the wMNE technique is robust to noise in EEG data and offers a head model with fair spatial resolution (Baillet et al., 2001). The estimated source current strength – as a function of time at each of the 3 x 5005 vertices of the cortex surface – was obtained by multiplying the EEG time series at each electrode by the wMNE inverse operator. This linear operation allows performing time-frequency analyses directly on the source space (Ambrosini & Vallesi, 2016), which was done by using complex Morlet wavelets as outlined before. Results were averaged across trials for each condition, and normalized based on Brainstorm's implemented *z*-score transformation relative to the -500 to -200 ms pre-trial baseline. *Z*-scores for theta power (4-8 Hz) were rectified to detect absolute power changes above baseline. Source estimates of theta power were analyzed during the post-feedback 300-500 ms window.

Time-frequency phase synchrony analyses

Theta phase synchrony was measured by calculation of the phase-locking factor (PLF; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). The PLF reflects the extent to which phase angles take on similar values across trials, and varies between 0 (absence of phase synchrony) and 1 (perfect phase synchrony) (Lachaux, Rodriguez, Martinerie, & Varela, 1999; Tallon-Baudry et al., 1996).

Event-related brain potential analyses

To investigate the FRN, artifact-free epochs were further segmented to 1200 ms windows including a 200 ms pre-feedback interval, which was used for baseline correction. Amplitude detection of the FRN was similar to our previous ERP studies using the SJP (Dekkers et al., 2015; Van der Molen et al., 2014). A peak-to-peak detection method was employed by subtracting peak amplitude of the P2 component (200-300 ms) from the most negative peak that followed the P2 (250-350 ms). This method is in line with other FRN studies (Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003) and reduces overlap of brain potential components surrounding the FRN.

Statistical analyses

Statistical analyses were carried out in IBM Statistics (version 23, IBM corporation, 1989-2011) for time-frequency theta power and phase synchronization, as well as FRN analyses. EEG measures were log-transformed and separately entered into a Site (2 levels: Fz, FCz) x Expectancy (2 levels: Expected, Unexpected) x Valence (2 levels: Acceptance, Rejection) repeated-measures Analysis of Variance (ANOVA). Greenhouse-Geisser correction was applied whenever appropriate, but uncorrected degrees of freedom are reported for transparency. All post-hoc comparisons were Bonferroni corrected for multiple comparisons.

Statistical analysis of source-localization of feedback-related theta power data was performed using nonparametric cluster-based permutation tests (Maris & Oostenveld, 2007). This type of nonparametric testing controls for type 1 error rate in the context of multiple comparisons by identifying clusters of significant source activity. Normalized source data were averaged over time (300-500 ms post-feedback) and frequency (4-8 Hz), thus statistical analyses only considered the spatial dimension of the cluster analysis. The Monte-Carlo method for statistical testing with paired t-tests was employed. The permutation distribution of cluster-level statistics was approximated by drawing 1000 random permutations of the source data. The cluster method for multiple comparisons was used and alpha was set at 0.05.

Results

Behavioral analysis

As in prior studies (Dekkers et al., 2015; Gunther Moor et al., 2010; Van der Molen et al., 2014; Van der Veen et al., 2014), participants were slightly biased in their expectancies of the outcome of social evaluation. That is, participants predicted social acceptance feedback on 55.71% (SD = 8.58) of the trials, which differed significantly from 50%, $t(55) = 4.98$, $p =$ <

.0001. A paired samples t-test indicated that the speed of judgments did not differ between social acceptance and rejection expectancies (mean difference = 2.51 ms, $t(55) = .29$, $p = 0.77$). Behavioral data are presented in Table 2.

--- insert Table 2 about here ---

Theta power

The ANOVA on theta power yielded a main effect of Site, $F(1,55) = 12.18$, p = .001. $\eta_p^2 = .18$. Theta power was significantly larger at Fz than at FCz (mean difference = .27; SEM = .06). In addition, main effects were found for Valence, $F(1,55) = 6.39$, p = .014. $\eta_p^2 = .10$, and Expectancy, $F(1,55) = 6.79$, p = .012. $\eta_p^2 = .11$, which were included in a significant Valence x Expectancy interaction, $F(1,55) = 5.91$, p = .018, $\eta_p^2 = .11$. Decomposition of this interaction effect indicated that theta power was significantly highest for unexpected social rejection feedback relative to the other feedback conditions (all other *p*'s > .05). Theta power for the four social feedback conditions is plotted in Figure 2 for the Fz electrode, as theta power was largest at this lead.

--- insert Figure 2 about here ---

Source-localization analysis

We explored the neural sources underlying the theta power burst associated with the processing of unexpected rejection feedback and compared these estimated sources to the source activity associated with the other feedback conditions. Figure 3 presents the source maps displayed on the cortex for the four feedback conditions. As can be verified, a notable increase in theta-related brain activity was observed over midfrontal regions during the processing of unexpected social rejection feedback. More specifically, the source analyses suggested that for all conditions, the main probable source of theta power was located in the ACC and was most prominent in the unexpected rejection condition. Cluster-based nonparametric testing yielded significant differences in source activity between the unexpected rejection condition and the other feedback conditions. As shown in Figure 4, the two contrasts between unexpected rejection with the two congruent feedback conditions resulted in a similar pattern of significant source differences. For both contrasts, significant source differences (*p*'s < .01) were observed for regions encompassing the dACC (BA 32), the frontal pole (BA 9 and 10), the inferior frontal gyrus / insula (BA 44 and 45), the left supplementary motor area (BA 6), and the subgenual cingulate (BA 25). These results indicated significantly higher theta power in these brain regions. Cluster-based permutation testing for the contrast unexpected rejection with unexpected acceptance revealed a significant difference ($p < .05$) in source activity in regions encompassing the right frontal pole (BA 9 and 10), the dACC (BA 24) and the supplementary motor area (BA 6), suggesting a significant increase in theta power in these brain regions.

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Inter-trial theta phase synchrony

The ANOVA on inter-trial theta phase synchrony yielded a main effect of Valence, $F(1, 55) = 8.27$, $p <.01$, $\eta_p^2 =.13$, indicating significantly stronger theta phase synchronization for social rejection than social acceptance feedback (mean difference = .02; SEM = .01). Further, a main effect was found for Expectancy, $F(1, 55) = 6.84$, $p = .01$, $\eta_p^2 =.11$. Theta phase synchrony was stronger for unexpected than for expected social evaluative feedback (mean difference =.02, SEM = .01). Other main and interaction effects were not significant (*p*'s > .05).

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Brain potential analysis

The ANOVA on FRN amplitude yielded a main effect Site, *F*(1,55) = 5.41, *p* = .02, η_p^2 =.09. FRN amplitude was significantly larger at FCz than at Fz (mean difference = -1.70, SEM = .66). In addition, the main effect of Expectancy, *F*(1,55) = 9.92, *p* = < .01, η_p^2 = .15, indicated that FRN amplitudes were significantly larger for unexpected than expected feedback (mean difference = .12; SEM = .01). Other main and interaction effects were not significant (*p*'s > .05). The FRN findings are presented in Figure 5, and peak amplitude is presented for the FCz electrode since the FRN was maximal at this lead.

--- insert Figure 6 about here ---

Discussion

The goal of this study was to examine theta oscillatory reactivity to social evaluative feedback processing. Results revealed that social rejection feedback elicited a pronounced increase in midfrontal theta power, but this effect was only observed when social rejection feedback was unexpected. This increase in theta power during unexpected social rejection feedback could be source-localized to brain regions typically reported during activation of the saliency network (i.e., the dACC, insula, inferior frontal gyrus, frontal pole, and supplementary motor area (SMA)) (Crottaz-Herbette & Menon, 2006; Menon & Uddin, 2010; Sridharan, Levitin, & Menon, 2008). For theta phase dynamics we observed a significant effect of feedback valence, namely, social rejection feedback yielded stronger inter-trial theta phase synchrony than social acceptance feedback. Moreover, theta phase dynamics mimicked the behavior of the FRN elicited by social feedback. That is, like the FRN, theta phase synchrony was strongest for unexpected feedback. Together, this study is the first to report on neural oscillatory dynamics during social evaluative feedback processing, and highlights distinct roles for theta power and phase in its sensitivity to valence and expectancy of social evaluative feedback.

A major finding of this study refers to the significant increase in theta power when participants received unexpected social rejection feedback. Specifically, theta power differed from both inter-trial theta phase synchrony and FRN amplitude by being exclusively sensitive to unexpected social rejection feedback. This result suggests that social rejection feedback is only processed as a potential social threat when this feedback comes as a surprise to the individual, a finding that adds to the growing literature suggesting an important role of theta oscillatory power in processing cues that convey social threat (Cristofori et al., 2013; Van Noordt et al., 2015). Specifically, Van Noordt et al. (2015) demonstrated that the midfrontal theta response during the earlier stages (200-400 ms) of social exclusion differed from the later stages (400-800 ms) with regard to the neurocognitive processes that this theta burst reflects. Interestingly, the later burst in theta power was positively correlated with self-reported ostracism distress, whereas this correlation was absent during the earlier theta burst. In contrast, the early theta burst might have reflected a manifestation of a ‘threat detection’ mechanism, and perhaps similar to the neurocognitive processes indexed by theta power in the current study. That is, increased sensitivity to social threat, but only when this threat is unexpected. It has been argued that social exclusion in Cyberball might violate the participant’s expectancies about receiving the ball and the increase in brain activity in response to social exclusion might also be due to expectancy violation rather than processing of social exclusion per se (cf., Dekkers et al., 2015; Somerville et al., 2006; Van der Veen et al., 2014). Indeed, Van Noordt et al. (2015) posited that the influence of expectancy violations on neural reactivity is particularly evident during the early theta response in Cyberball's exclusion block, a notion that is in line with the current data. Here we demonstrate an early responsivity of theta power during the processing of unexpected social rejection feedback with a temporal similarity to the early theta burst reported in the Van Noordt et al. (2015) study. The emotional distress experienced by being rejected by someone you like (or excluded from a meaningful interaction) might be captured by theta power during later stages of information processing. Our results did not yield evidence of this prolonged duration of theta oscillatory reactivity as in Cyberball studies, but this effect is most likely due to the repeated presentation of social exclusion trials that induces this slow wave activity. However, it should be noted that a direct comparison of findings between Cyberball and the SJP is complicated by important differences between the two paradigms. Although both paradigms introduce participants to a socially threatening condition that might lead to social disconnection (e.g., being rejected by peers or being excluded from a group), the SJP indexes neurocognitive processes implicated in *social rejection*, whereas Cyberball examines *social exclusion*. In the SJP participants receive feedback on whether they are liked or disliked by unknown peers, and participants are asked to predict the outcome of this social evaluative process. In Cyberball, social threat is induced by excluding participants from participating in a group, which introduces an ambiguous situation to the participant whom might not only experience a different set of emotions than in the SJP, these emotions might also differ throughout the exclusion block (ranging from initially feeling annoyed to feelings of social hurt during later stages of the paradigm).

Our current theta power results match previous observations of a significant slowing of heart rate when participants were unexpectedly rejected by their peers in the SJP (Dekkers et al., 2015; Gunther Moor et al., 2010; Van der Veen et al., 2014). This significant slowing of heart rate was interpreted to reflect an ‘autonomic signature’ of processing social rejection, and a manifestation of a neural network involved in the processing of expectancy violations, which is assumed to subsequently potentiate perceptual responsiveness making a potentially threatening cue more salient (e.g., Markovic, Anderson, & Todd, 2014). The current EEG results highlights the possibility of a common mechanism (i.e., midfrontal theta dynamics) by which the brain communicates with the central autonomic network (Thayer & Lane, 2000) in response to social threat. An important neural node within this network is the ACC, which also appeared to be the dominant source of theta power in response to social evaluation in all feedback conditions. However, the neural sources governing the observed increase in theta power elicited by unexpected rejection feedback showed a more widespread activation pattern, including the ACC and frontal pole. Cluster-based permutation contrasts between the unexpected rejection condition with the two congruent feedback conditions (expected acceptance and expected rejection) revealed significant differences that could be localized to probable sources including the ACC, frontal pole, SMA, inferior frontal gyrus and insula – brain regions that constitute the saliency network (Ham, Leff, de Boissezon, Joffe, & Sharp, 2013; Menon & Uddin, 2010; Sridharan et al., 2008). Increased activation of these regions is consistent with theoretical views on the functional significance of the saliency network to assist in targeting relevant brain regions in order to guide behavior. For example, Menon and Uddin (2010) postulated that within the saliency network, the insula acts as an integrative hub that receives bottom-up deviancy signals from sensory areas, selectively amplifies the saliency of these events, and transmits this information to the ACC for further processing (see also, Crottaz-Herbette & Menon, 2006). It has been argued that the dACC plays a key role in allocating cognitive control based on an evaluative process that estimates whether it is worth investing control in a task (Shenhav, Botvinick, & Cohen, 2013). This evaluative aspect of the dACC has been dubbed *Expected Value of Control* (EVC), and can be understood in terms of monitoring and specification processes. First, the dACC monitors the saliency signals to estimate the EVC. Thereafter, the dACC specifies the required cognitive-behavioral adjustments by activating other neural systems that can implement these required adjustments. Although this interpretation is speculative, the EVC model could also help explaining why we did not find any significant differences in the paralimbic regions in the social feedback contrast between unexpected rejection and unexpected acceptance, but *did* find increased activity in probable sources such as the dACC, frontal pole and SMA. Namely, both conditions would trigger the saliency system because unexpected social evaluative feedback is categorized as a mismatch between participants' expectancies about the feedback outcome and the actual feedback. However, the dACC would rate the EVC as higher for unexpected rejection feedback than for unexpected acceptance feedback, since only the former would pose a significant threat to the individual.

The above interpretation is in line with social belongingness theory (Baumeister & Leary, 1995). That is, unexpected rejection feedback can be interpreted to pose a threat to social belongingness, and the currently observed neural substrates governing theta power enhancement after unexpected rejection feedback could reflect activation of the social threat monitoring system to protect people from social isolation. The neural underpinnings of this social threat monitoring system is likely to show overlap with those brain structures implicated in the saliency network. Indeed, the relevance of this saliency network in the processing of social threatening information has been previously acknowledged in studies on social anxiety (cf., Miskovic & Schmidt, 2012), and recent meta-analytic evidence suggests that midfrontal theta oscillations play a significant role in cognitive control operations aimed at reducing uncertainty and anxiety (Cavanagh & Shackman, 2015). Interestingly, recent intracranial work by Smith et al. (2015) corroborated the ACC as the main generator of feedback-related frontal theta power, and its role in relaying theta rhythms to important neural regions implicated in cognitive control, and possibly also affective control. Although future work should better parcel the exact contribution of the neural regions activated by social evaluative feedback, our current work suggests that next to the ACC, other regions within the saliency network – such as the insula – might play an important role in generating these feedback-related theta rhythms.

Notably, the current examination of theta oscillatory power and phase dynamics resulted in a distinct pattern of findings regarding their functional significance in social feedback processing. As theta power was exclusively sensitive to unexpected social rejection feedback, we observed that inter-trial theta phase synchrony was higher for social rejection feedback than for social acceptance feedback. In addition, theta phase synchrony was enhanced when participants received social feedback that was unexpected, irrespective of its valence. These findings suggest that theta phase is entrained by negatively valenced social evaluative feedback, as well as feedback that communicates cognitive conflict (i.e., expectancy violation), which corroborates studies reporting on increased theta phase synchrony during processing of negative performance feedback or cognitive conflict (e.g., error monitoring) (Nigbur, Cohen, Ridderinkhof, & Sturmer, 2012; Van Driel, Ridderinkhof, & Cohen, 2012).

In future studies it would be interesting to validate the current results in both male and female participants, and further examine the specificity of midfrontal theta power to the processing of unexpected rejection feedback. Importantly, since our current design did not allow for dissociating unexpected social rejection feedback from a more common mechanism implicated in processing unexpected *negative* feedback, some caution is warranted with regard to the functional role of midfrontal theta power in the processing of *social rejection* feedback. In addition, future investigations should examine how theta oscillatory activity –

induced by unexpected social rejection feedback – influences subsequent social decision-making. For example, social bargaining studies have linked the magnitude of theta oscillatory power to the degree of unexpectedness of feedback (Billeke, Zamorano, Cosmelli, & Aboitiz, 2013; Billeke et al., 2014). These studies suggested that theta oscillations play an important role in the fine-tuning of behavioral strategies during social interactions. Albeit speculative, the currently observed increased levels of theta power during processing of unexpected social rejection feedback could reflect a 'worse-than expected' outcome that would influence the way someone would behave in a social context. The requirement for adjusting behavioral strategies in a social context might induce atypical patterns of midfrontal theta power in anxious individuals (Cavanagh & Shackman, 2015), specifically in those whom are sensitive of social evaluation.

In conclusion, this study yielded an interesting dissociation between midfrontal theta power and the time-locked feedback components in the EEG (i.e., inter-trial phase synchrony and the FRN). Specifically, we have shown that social rejection feedback is associated with enhanced power of theta oscillations, but only when this feedback is unexpected. These data on midfrontal theta oscillatory activity during social feedback processing offers an interesting window for future studies to better understand the functional significance of theta reactivity in social-emotional decision-making paradigms, as well as the neurocognitive mechanisms implicated in psychopathological disorders characterized by rejection sensitivity.

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Table Legends

Table 1. Average number of artifact-free EEG segments (SD) that have been used for the analyses.

Table 2. Average number of trials (SD) and response time (SD) for the 56 participants in the Social Judgment paradigm. Averages are presented for predicted social acceptance feedback (“Yes”) and predicted social rejection feedback (“No”).

Figure Legends

Figure 1. Example of a single trial of the Social Judgment paradigm.

Figure 2. Time-frequency power at Fz during the 300-500 ms post-feedback interval. (A) Time-frequency plots reveal a prominent increase in theta power (4-8 Hz) in the unexpected social rejection condition. (B) Scalp distribution of theta power during social evaluative feedback processing showing a midfrontal dominance. (C) Theta power was significantly higher in the unexpected social rejection condition relative to the other feedback conditions. Yes-Yes = expected acceptance; Yes-No = unexpected rejection; No-No = expected rejection; No-Yes = unexpected acceptance. Error bars indicate SEM.

Figure 3. Theta oscillatory power source-localization maps during the 300-500 ms post-feedback interval. Depicted are mid-sagittal slices (left and right) of theta power activation associated with the processing of social evaluative feedback. The source activation maps are based on activation of at least 40 vertices (amplitude threshold of 50%).

Figure 4. Contrast maps of theta source activity for unexpected rejection feedback with the other social feedback conditions. Depicted are the scalp topographies, as well as the mid-sagittal slices (left and right) and axial views of the three contrasts. Only those clusters of source activity are shown that survived cluster-based nonparametric permutation testing.

Figure 5. Inter-trial theta phase synchrony during the 300-500 ms post-feedback interval. (A) Similar to theta power, inter-trial theta phase dynamics displayed a midfrontal dominance in activation. (B). Time course of theta phase synchrony level displayed for all four conditions, as well as average phase synchrony values per condition, and the main effects of Valence and Expectancy. (C) Scalp maps displaying theta phase synchrony during the 300-500 ms interval for the four feedback conditions. Yes-Yes = expected acceptance; Yes-No = unexpected rejection; No-No = expected rejection; No-Yes = unexpected acceptance. Error bars indicate SEM.

Figure 6. Event-related brain potentials elicited by social evaluative feedback at FCz. (A) Event-related brain potentials displaying the FRN for the four feedback conditions. (B) Average FRN amplitude per feedback condition. (C) Main effects of Valence and Expectancy on FRN amplitude. Yes-Yes = expected acceptance; Yes-No = unexpected rejection; No-No = expected rejection; No-Yes = unexpected acceptance. Error bars indicate SEM.

TABLES

Table 1.

Condition	Trials (SD)	Range (min.-max.)
Yes-Yes	35.46 (7.53)	20-53
Yes-No	34.73 (8.52)	18-53
No-No	28.71 (7.95)	14-48
No-Yes	28.41 (7.00)	16-44

Table 2

Condition	Trials (SD)	Response time (SD)
Yes	81.73 (12.52)	1426.95 (272.93)
Yes-Yes	40.84 (6.69)	
Yes-No	40.89 (8.47)	
No	65.02 (12.84)	1429.46 (257.58)
No-No	32.46 (8.28)	
No-Yes	32.55 (6.99)	

Note: Trials on which participants did not respond or responded too late, were omitted from this overview and further analyses. Yes-Yes = expected acceptance; Yes-No = unexpected rejection; No-No = expected rejection; No-Yes = unexpected acceptance.