Running Head: EMOTION AND EXPECTATIONS IN SCHIZOPHRENIA

Title: Neural correlates of dynamic emotion perception in schizophrenia and the influence of prior expectations

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Abstract

Impaired emotion perception is a well-established and stable deficit in schizophrenia; however, there is limited knowledge about the underlying aberrant cognitive and brain processes that result in emotion perception deficits. Recent influential work has shown that perceptual deficits in schizophrenia may result from aberrant precision in prior expectations, associated with under-activity in regions such as the frontal cortex. In the present study, we investigated the perception of dynamic, multisensory emotion, the influence of prior expectations and the underlying aberrant brain processes in schizophrenia. During a functional Magnetic Resonance Imaging scan, participants completed the Dynamic Emotion Perception task, which induces prior expectations with emotion instruction cues. We delineated neural responses and functional connectivity in whole-brain large-scale networks underlying emotion perception. Compared to healthy individuals, schizophrenia patients had lower accuracy specifically for emotions that were *congruent* with prior expectations. At the neural level, schizophrenia patients had less engagement of right inferior frontal and parietal regions, as well as right amygdala dysconnectivity during discrimination of emotions congruent with prior expectations. The results indicate that individuals with schizophrenia may have aberrant prior expectations about emotional expressions, associated with under-activity in inferior frontoparietal regions and right amygdala dysconnectivity, which results in impaired perception of emotion.

Keywords: schizophrenia; naturalistic emotion; prior expectations; functional connectivity; inferior frontal gyrus; right amygdala.

1. Introduction

Emotion perception is impaired in schizophrenia (SCZ) with a significant impact on overall functional outcome (Irani et al., 2012). Currently, there is inadequate knowledge of the cognitive and neural processes underlying emotion perception difficulties in SCZ. The 'Predictive Coding' theory of perception proposes that our brain continually generates predictive models of the world, based on prior expectations (generated from previous experiences) and new sensory information (Friston and Kiebel, 2009; Friston et al., 2006). Under this theory, emotional information that is congruent with prior expectations is processed more efficiently, as prior expectations direct attentional focus and decrease processing resources (Barbalat et al., 2013; Brown and Brune, 2012). For example, prior expectations have been found to improve speed and accuracy during emotion discrimination in healthy individuals (Barbalat et al., 2013; Dzafic et al., 2016). Within the Predictive Coding theory, SCZ has been conceptualized as a disorder of aberrant precision (certainty) in prior expectations. However, there is conflicting evidence whether patients with SCZ have reduced (Adams, Huys, & Roiser, 2016; Chambon et al., 2011; Dima, Dietrich, Dillo, & Emrich, 2010) or increased precision in prior expectations (Alderson-Day et al., 2017; Powers, Mathys, & Corlett, 2017; Teufel et al., 2015). Reduced precision in prior expectations can lead to inefficient directing of attention and nosier incoming sensory information. In contrast, increased precision in prior expectations has been implicated in psychotic experiences, such as hallucinations. In the current study, we investigated whether aberrancy in prior expectations leads to impaired recognition of dynamic, audio-visual emotion in patients with SCZ.

Processing of emotions that are congruent with prior expectations is associated with activity in frontal areas (Barbalat et al., 2013) and the amygdala (Dzafic et al.,

2016). Aberrant precision in prior expectations in SCZ has been proposed to reflect impaired activity in frontal regions, resulting in aberrant inhibitory top-down influence over primary sensory regions (Adams et al., 2016). This is compatible with the considerable evidence for frontal dysfunction in SCZ (Fan et al., 2013; He et al., 2013; Huang et al., 2010) and hyper-connectivity in sensory regions (Anticevic et al., 2014). In addition to frontal dysfunction in SCZ, several converging lines of evidence have found that deficits in emotion perception are associated with dysconnectivity in functional networks involving the amygdala (Bjorkquist et al., 2016; Das et al., 2007; Mukherjee et al., 2012). However, no study to date has directly explored the neural circuitry underlying aberrant prior expectations in SCZ during emotion perception. In the current study, we investigated if attenuated prefrontal activity and rAMY dysconnectivity in SCZ are associated with impaired perception of emotions congruent with prior expectations.

In summary, our aim was to investigate the influence of prior expectations on naturalistic emotion perception in SCZ, and the underlying distinct patterns of brain activity, and functional connectivity with the rAMY. The effect of prior expectations on emotion perception in SCZ has only been investigated using static emotion displays (Barbalat et al., 2012), despite that sensory information in emotional expressions is dynamic in nature and often changes rapidly in social situations. Naturalistic emotion displays may better capture the complex neural processes associated with emotion perception (Arsalidou et al., 2011). In line with previous studies (Hargreaves et al., 2016; Johnston et al., 2010) we predicted that SCZ patients would have deficits in discriminating dynamic emotion perception in general, with greater deficits compared to healthy controls when emotion perception relies on prior expectations (Chambon et al., 2011); in other words, detecting emotions congruent

with prior expectations. At the neural level, we predicted reduced activation in frontal regions in patients with SCZ during emotion perception that is congruent with prior expectations (Anticevic et al., 2014; Barbalat et al., 2013). Finally, we predicted that SCZ patients would have greater difficulty using prior expectation to facilitate emotion perception (Chambon et al., 2011), as indexed by poorer accuracy and increased response times, and this would be associated with rAMY dysconnectivity.

2. Methods and Materials

2.1. Participants

Sixteen, right-handed patients with chronic SCZ (age range = 30-57; mean age = 46.40, SD = 9.43) were recruited from the Queensland Centre for Mental Health Research (QCMHR). Sixteen age and sex matched, right-handed healthy controls (HC; age range = 34-58; mean age = 45.19, SD = 7.92) were recruited from a National Health and Medical Research Council (NHMRC)-funded, population-based Australian sample of individuals as controls for the SCZ participants. The SCZ patients were comprehensively ascertained by trained clinicians using the Diagnostic Interview for Genetic Studies (DIGS) (Nurnberger et al., 1994), the Family Interview for Genetic Studies (FIGS) (Maxwell, 1992), and information extracted from all available medical records. Best Estimate Final Diagnosis (BEFD) (Leckman et al., 1982) was assigned by two experienced research psychiatrists independently, after reviewing all the available information then agreeing on a consensus diagnosis. Diagnostic inter-rater reliability was assessed using standard procedures (Suarez et al., 2006).

Prior screening confirmed that all participants were without eye disease, a history of neurological disorders, or metal implants in their body, and the HCs were

not currently taking medication. The Mini International Neuropsychiatric Interview (M.I.N.I.) version 5.0.0 (Sheehan et al., 1997) was used to screen participants who had current alcohol dependence and a major depressive episode. Intelligence quotient (IQ) was estimated using 2 subsets (vocabulary and matrix reasoning) of the Wechsler abbreviated scale of intelligence (WASI; Wechsler, 1999); please see Table 1 for demographic information. The healthy control group in this study had a high-average IQ, which was significantly higher than the patients. Thus, we conducted correlations between IQ and accuracy on the Dynamic Emotion Perception task to examine whether differences in IQ were influencing the participants' ability on the Dynamic Emotion Perception task, finding that IQ was not significantly associated with accuracy at discriminating emotions (see Table 1, Supplementary materials). All participants were provided with an information sheet, which included a full description of the study and an MRI information sheet, which included further details regarding the MRI procedure. After reading the document, written informed consent was obtained. This research was approved by the West Moreton Hospital and Health Service Human Research Ethics Committee, and the University of Queensland Human Research Ethics. Participants received $40 in department store vouchers for the neurocognitive testing and MRI.

[Please insert Table 1 here]

2.2. Materials and Procedure

Participants completed the Dynamic Emotion Perception (DEP) Task (Dzafic et al., 2016) during an fMRI scan. The DEP task involved viewing audio-visual videos of a female actor (duration: 3 sec) expressing three emotions (anger, happiness

and neutral) that were either congruent or incongruent with prior expectations. Angry, happy, and neutral expressions were chosen in this task as these three emotions represent the three valences: positive, negative, and neutral. In addition, patients with schizophrenia have previously demonstrated deficits identifying threat (Pinkham et al., 2014) and misattributing threat onto neutral expressions (Underwood et al., 2015). Prior expectations were induced in each experimental block by (1) displaying an emotion instruction cue at the start of each block, (2) displaying the emotion cue (without the instruction) before each video clip, in order to reinforce the instruction and to reduce the working memory load, and (3) by increasing the occurrence likelihood of emotional videos congruent with the emotion in the cues in each block.

At the beginning of each block, the participants were presented with an emotion instruction cue prompting them to make an "index finger press" whenever they saw a particular emotion, which was presented as both a still image and in writing (e.g., "HAPPY") underneath the instruction text. Thereafter the participants were presented with emotion videos and repeating emotion cues (without the instruction text). Within an experimental block, the cue was always one emotion (e.g., Angry block: an angry instruction cue, followed by a happy video (incongruent), then an angry cue followed by, for example, an angry video (congruent), then an angry cue followed by another angry video (congruent), then an angry cue followed by a neutral video (incongruent) etc.). However, videos within a block would alternate in emotion (e.g. an Angry block of six videos, would contain four angry videos, one happy video and one neutral video, which were presented in a random order). The participant was instructed to make an index finger press when the emotion in the video was congruent with the emotion cue, or to make a middle finger press when the emotion in the video was incongruent with the emotion cue (for more details, see Dzafic et al., 2016).

Prior to the fMRI experiment, participants were trained with a practice task outside the MRI scanner. Both the practice task and fMRI task were presented using E-Prime 2.0 software (https://www.pstnet.com/eprime.cfm, 2013; Schneider et al., (2012)) on a Windows computer screen. Responses were made on a custom-built MR-compatible response box. Participants were instructed to respond as quickly and as accurately as possible. The trials in the fMRI experiment contained 18 conditions (3 emotion videos x 2 congruency x 3 runs). Following the fMRI experiment participants completed the WASI questionnaire (Wechsler, 1999). The practice task, fMRI task, and questionnaire were completed at the Centre for Advanced Imaging, University of Queensland's 3T scanner facility.

2.3. MRI Procedure and Preprocessing

Structural and functional MRI images were acquired by a 3T Siemens Magnetom TrioTim system using a 12-channel head coil. The scans collected for each participant were as follows: localizer, T1-weighted anatomical image MP2-RAGE sequence (repetition time (TR): 1900 ms, echo time (TE): 2.32 ms, resolution: 1 mm^3, FoV: 230 mm, 192 slices, inversion time (TI): 900 ms, flip angle: 9 degrees), whole-head T2*-weighted echo-planar sequence (TR: 3000 ms, TE: 30 ms, resolution: 2.5 mm^3, slices: 46, FoV: 192 mm, flip angle: 90 degrees), DWI (TR: 8400 ms, TE: 100 ms, resolution: 2.3 mm x 2.3 mm x 2.5 mm, slices: 60, FoV: 300 mm, b-value: 2000 s/mm^2, directions: 64), and resting-state (TR: 3000 ms, TE: 30 ms, resolution: 2.5 mm^3, slices: 46, FoV: 192 mm). The total scanning time per session was 45min.

Standard preprocessing of the images was carried out using Statistical Parametric Mapping (SPM8; http://www.fil.ion.ucl.ac.uk/spm/software/spm8, 2013; Friston (2003)). The preprocessing steps were as follows: slice timing on the

functional images, to correct for differences in slice acquisition times within each volume using the middle slice as reference; realignment (estimate and reslice) on the functional images, to correct for inter-scan movement within each run (no participant was excluded for excessive movement (defined as >3 mm translation, >2 degrees rotation); co-registration of the functional and structural images; segmentation of the structural image, with heavy regularisation (0.1) recommended for MP2-RAGE sequence; normalization of the resliced images into a standardized, stereotaxic space (according to the Montreal Neurological Institute template); and smoothing of normalized images with a 8mm full-width-at-half-maximum isotropic Gaussian kernel.

3. Data analysis

3.1. Behavioural Analyses

Discriminability was calculated using *d'* scores (*d*' = z(Hits) - z(False Alarms)) (Macmillan and Creelman, 1990) to assess emotion discriminability for each participant. For this calculation, we adjusted *d'* according to Corwin (1994) where Hit rate = 1 or False alarm = 0. We conducted a two-way factorial ANOVA to investigate differences between SCZ and HC in discriminability for each emotional video (angry, happy, and neutral).

Mean reaction times (RTs) and accuracy percentage from all responses acquired during scanning were calculated for each participant, across 18 conditions (3 emotion videos x 2 congruency x 3 runs). Only RTs for correct responses were retained for the analysis. Trials from blocks in which accuracy was less than 50% (chance performance) were removed from further analyses. Missed trials were treated as incorrect in the calculation of accuracy percentages.

Two types of factorial mixed-subjects ANOVAs were conducted on RTs and percentage accuracy. First, a three-way ANOVA was conducted to investigate the effect of prior expectations on emotion videos in SCZ compared to HCs, with factors: 3 emotion videos (angry, happy, neutral) x 2 congruency (congruent and incongruent) x 2 group (SCZ and HC). Next a three-way ANOVA was conducted to investigate the effect of prior expectations across time (experimental runs) in SCZ compared to HCs, with factors: 3 experimental runs (run 1, run 2, run 3) x 2 congruency (congruent and incongruent) x 2 groups (SCZ and HC). In addition, we conducted Pearson's correlations between accuracy and RTs on the DEP task and SCZ positive and negative symptoms (using total SAPS and SANS scores). In order to examine whether negative or positive symptoms influenced SCZ participants' ability on the different conditions of the DEP task.

Finally, we examined omissions for congruent and incongruent conditions. A two-way ANOVA was conducted to investigate the effect of prior expectation on omissions in SCZ compared to HCs, with factors: 2 congruency (congruent and incongruent) x 2 group (SCZ and HC).

All behavioural analyses were conducted using the SPSS package (SPSS Inc., Armonk, NY). Significant interactions were further analysed using Bonferroni corrected repeated contrasts, independent samples t-tests, and paired samples t-tests. Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity where the assumption of sphericity had been violated. Any outliers, as defined by z-score > 3, were removed from further analyses. This resulted in the removal of one SCZ and one HC from the discriminability analysis, and two SCZ and one HC from the accuracy analysis.

3.2. fMRI Whole-Brain Analysis

The goal of the analysis was to investigate the regionally specific responses in SCZ compared to HC during congruent and incongruent conditions, as well as the association with SCZ symptom scores and brain activity. Functional data were analysed using a general linear model for event-related designs in SPM8. At the first level, the onsets for the videos were selected as the event onsets and the videos were separated into 6 different conditions: angry congruent video, angry incongruent video, happy congruent video, happy incongruent video, neutral congruent video, and neutral incongruent video. Head motion parameters were included as a regressor to account for participant motion during the course of the experiment. A 1/128 Hz high-pass filter was used to remove slow signal drifts, and a canonical HRF with no derivatives was selected. Contrast images were entered into a second-level analysis using a full factorial model, with factors: group (SCZ vs. HC) and congruency (congruent and incongruent). T-test models examined the brain activity differences in SCZ vs. HC during congruent and incongruent conditions, separately. We included response accuracy and IQ as covariates in the analysis. In addition, we conducted a multiple regression analysis with SANS and SAPS scores as the predictor and brain activity as the outcome. We included IQ as a covariate in the analysis. Only voxel-level or cluster-level $p < 0.05$ family-wise error (FWE) corrected clusters of $k < 10$ voxels were considered.

3.3. Functional Connectivity and Brain-Behaviour Analysis

Functional connectivity during the DEP task and its relation to response speed was assessed using a multivariate, partial least squares (PLS) approach (McIntosh et al., 1996). The selection of the right amygdala (rAMY) region was literature driven

(Dzafic et al., 2016) and based on our findings from a previous study with a different group of healthy controls. We correlated activity in the rAMY [18 -8 -18] region with activity in the rest of the brain, and with response time scores of the participants in the congruent and incongruent conditions. Specifically, the procedure involved extracting the blood-oxygen-level dependent (BOLD) values in the rAMY from SPM8 analysis, from the onset of each video, and then in PLS correlating these scores with activity in all other brain regions, and response times. This was done for each condition across all participants to form correlation maps. Next, the correlation maps were decomposed with singular value decomposition (SVD), resulting in a set of orthogonal variables (latent variables; LVs). Each LV consists of three components: singular values (significance for a given LV, determined by conducting 500 permutations), voxel saliences (spatiotemporal activity for a given LV, reliability assessed by conducting bootstrapping 100 times), and task saliences (degree to which each condition is related to the brain-seed correlations within the given LV) (McIntosh et al., 1996). For each LV, "brain scores" are computed, which indicate the degree to which each participant shows the pattern of brain activity identified. We calculated the correlation between the brain scores and the rAMY BOLD values to assess the relation between the whole-brain pattern and activity in the rAMY. Peak voxels with a bootstrap ratio > 3 and cluster size of 100 or more voxels were considered to be reliable, as this approximates $p < 0.001$.

4. Results

4.1. Behavioural Findings – Emotion Discriminability

A factorial ANOVA 3 (emotion video) x 2 (group) on discriminability *d'* showed a significant main effect of group, $F(1, 28) = 11.30$, $p = 0.002$, indicating that

SCZ have a lower discriminability compared with HC across different emotions. There was also a trend for an interaction between group and emotion, $F(2, 56) = 2.65$, $p = 0.079$ (see Fig. 1c).

4.2. Behavioural Findings – Prior expectations on emotion perception

A factorial ANOVA 3 (emotion video) x 2 (congruency) x 2 (group) on percentage accuracy revealed a main effect of group, $F(1, 27) = 7.88$, $p = 0.009$, SCZ ($M = 93.9\%$, *S.E.* = 0.01) had lower overall accuracy compared with HC ($M = 97.9\%$, *S.E.* = 0.01). There was a significant interaction between group and congruency, $F(1,27) = 4.64$, $p = 0.04$; independent samples t-tests revealed that SCZ patients, compared to HC, were significantly worse at detecting *congruent* emotions (*Ms(S.E.)*: SCZ = 92%(1.5); HC = 97.8%(1.4)), $t(17.23) = -2.74$, $p = 0.014$); however, SCZ patients were not significantly different at detecting incongruent emotions ($M = 95.8\%$, *S.E.* = 0.7) compared to HC ($M = 98\%$, *S.E.* = 0.7), $t(16.03) = -1.95$, $p = 0.07$ (see Fig. 1a). In addition, paired samples t-tests revealed that only SCZ patients were significantly worse at detecting congruent compared to incongruent emotions, $t(13) = -2.42$, $p = 0.031$), whereas, HC had similar accuracy across congruent and incongruent conditions, $t(14) = -0.26$, $p = 0.79$ (see Fig. 1a).

The factorial ANOVA on RTs revealed a main effect of group, $F(1, 29) = 19.48$, $p < 0.001$. Individuals with SCZ ($M = 1592.15$, *S.E.* = 90.64) were slower than HC ($M = 1035.39$, *S.E.* = 87.76) in the overall experiment. There was a significant interaction between group and emotion video, $F(1.55, 44.83) = 5.67$, $p = 0.01$. Independent samples t-tests revealed that SCZ patients compared to HC were significantly slower at detecting happy (*Ms(S.E.)*: SCZ = 1549.74(91.62); HC = 1024.72(88.71)), neutral (*Ms(S.E.)*: SCZ = 1760.13(98.62); HC = 1097.84(95.49))

and angry (*Ms(S.E.)*: SCZ = 1466.57(90.15); HC = 983.62(87.29)) videos compared to HCs, $p < 0.001$.

There were no correlations between SCZ symptoms and accuracy for incongruent emotions (SANS: $p = 0.21$; SAPS: $p = 0.62$), accuracy for congruent emotions (SANS: $p = 0.26$; SAPS: $p = 0.77$), RTs for incongruent emotions (SANS: $p = 0.16$; SAPS: $p = 0.40$), or RTs for congruent emotions (SANS: $p = 0.15$; SAPS: $p = 0.23$).

4.3. Behavioural Findings – Prior expectations over time

A factorial ANOVA 3 (experimental run) x 2 (cue) x 2 (group), on percentage accuracy revealed a significant interaction between group and run, $F(2,54) = 5.46$, $p = 0.007$. Paired samples t-tests revealed that while HC had a stable accuracy across runs, SCZ patients were significantly worse during the first and third runs (*Ms(S.E.)*: Run1 = 92.2%(0.01); Run3 = 94.1%(0.01)) compared to the second run ($M = 95.8\%$, S.E. = 0.01), $t(13) = -5.87$, $p < 0.001$ and $t(13) = 2.92$, $p = 0.012$, respectively (see Fig. S1c).

The factorial ANOVA on RTs revealed a significant interaction between group, run, and congruency, $F(1.77, 52.98) = 7.31$, $p = 0.002$. Paired samples t-tests revealed that SCZ patients improved in their detection speed for *incongruen*t videos from run 1 ($M = 1713.36$, S.E. = 112.99) to run 3 ($M = 1499.86$, S.E. = 90.89), $t(15) = 2.37$, $p = 0.03$, whereas HCs improved in their speed for *congruent* videos from run 1 ($M = 1195.47$, S.E. = 109.85) to run 3 ($M = 1027.99$, S.E. = 98.92), $t(15) = 3.85$, $p = 0.002$ (see Fig. S1d).

4.4. Behavioural Findings – Omissions

To assess whether the results were due to omissions we ran a factorial ANOVA 2 (congruency) x 2 (group), on trials in which the participant did not

respond. A significant main effect of group was found, $F(1, 27) = 4.35$, $p = 0.047$, indicating that SCZ missed more trials compared to HC. There was also a trend for an interaction between group and congruency, $F(1, 27) = 3.97$, $p = 0.056$ (see Fig. 1b).

[Please insert Figure 1 here]

4.5. fMRI Regional Activity Findings

Results from a full factorial analysis revealed a significant main effect of congruency with activations in the bilateral superior temporal gyri, left lingual gyrus, bilateral cuneus, right precuneus, right insula, bilateral inferior parietal lobule, left putamen, left precentral gyrus, right inferior frontal gyrus, and left primary somatosensory cortex. There was also a significant interaction between congruency and group with the activation in the right primary somatosensory cortex. Next, t-tests were conducted to examine the regionally specific responses in SCZ compared to HC during congruent and incongruent conditions separately. During *congruent* conditions (see Fig. 2a) SCZ recruited visual regions, whereas HC recruited right inferior frontal gyrus and bilateral inferior parietal lobule. During *incongruent* conditions (see Fig. 2b) SCZ recruited right precuneus, left fusiform gyrus, right cuneus, and right superior parietal lobule, whereas HC recruited right claustrum and globus pallidus (see Table 2). Finally, a multiple regression analysis was conducted for congruent and incongruent emotion videos with SANS and SAPS scores as the predictor variable. Our data show that an increase in SANS scores significantly predicted an increase in brain activity in the left insula during *congruent* videos (see Fig. 2c).

[Please insert Figure 2 & Table 2 here]

4.6. Functional Connectivity of Right Amygdala and Brain-Behaviour Findings

The functional connectivity analysis with rAMY identified one statistically significant LV (p = 0.012), accounting for 25.38% of covariance in the data (see Fig. 3). The LV differentiated two distinct expectancy-driven patterns of rAMY functional connectivity for SCZ and HC.

The first pattern of rAMY functional connectivity was observed during *incongruent* conditions for both SCZ and HC. Activity in this network was negatively correlated with response time, meaning that faster recognition of emotions incongruent with one's expectations was associated with stronger activation of this network in both HC and patients with SCZ. This large-scale network involved bilateral prefrontal regions, bilateral anterior and posterior cingulate gyri, left hippocampus, midbrain, bilateral occipital regions, bilateral parietal regions, bilateral insula, and thalamus (see Table 3).

Critically, the second pattern of rAMY functional connectivity was observed during *congruent* conditions, but *only* for HC. Activity in this network was negatively correlated with response times, meaning that faster recognition of emotions congruent with the HC's expectations was associated with stronger activation of this network. This network comprised rAMY, cingulate, caudate, parietal regions and thalamus (see Table 3).

[Please insert Figure 3 & Table 3 here]

5. Discussion

In the current study, we investigated dynamic emotion perception in patients with SCZ and the influence of prior expectations at the behavioural and neural levels. We identified reduced ability in SCZ patients to identify emotions that were congruently cued (i.e., congruent with prior expectations), as evidenced by poorer accuracy. At the neural level, we found reduced activity in right inferior frontal gyrus (IFG) and inferior parietal lobule, as well as rAMY dysconnectivity during congruent emotion trials. Furthermore, we found that during viewing of congruent videos greater negative symptoms predicted increased activity in the left insula. The findings show that although there is a general impairment during perception of dynamic emotions in SCZ, there is a more specific deficit in detecting emotion congruent with prior expectations. These findings suggest that there is an important link between emotion perception difficulties in SCZ and aberrancy in prior expectations.

Dynamic, audio-visual emotion perception was found to be impaired in patients with SCZ compared to healthy individuals, as demonstrated by poorer overall performance (lower accuracy, response speed, ability to discriminate emotional videos and greater omissions). This is in line with previous research showing that dynamic emotion perception is impaired in general in schizophrenia (Chan et al., 2010; Feingold et al., 2016; Hargreaves et al., 2016; Huang et al., 2013; Johnston et al., 2010) and may reflect domain-general deficits, such as poor attention. In addition, patients with SCZ had less activity in the superior temporal gyri, often implicated in audio-visual integration and representation of dynamic emotional expressions (Robins et al., 2009; Said et al., 2010). Interestingly, in addition to the general deficit in emotion perception, patients with SCZ had a more specific deficit in detecting emotions that were congruent with prior expectations, indicated by poorer accuracy. In comparison to the patients, healthy individuals were facilitated in their accuracy

and response times by prior expectations, over the course of the study for congruent emotions only. In the current study, due to the dynamic nature of the audio-visual emotional stimuli, congruence detection is initially (before priors develop) the more difficult condition, as the participant is evaluating whether the ever-changing, dynamic emotional content is congruent with the previous cue. This difficulty in congruence detection has been reported previously, especially when the task involves deliberate reasoning about the congruency between the cue and emotion (Dieguez-Risco et al., 2015; Dzafic et al., 2016). Therefore, the congruent condition in our task requires processes such as reasoning and associative learning, that reinforce prior expectations. These processes have been found to be impaired in patients with schizophrenia in previous literature (Diwadkar et al., 2008; Dudley et al., 2016; Green et al., 2004; Kruck et al., 2011). Our findings also support those of Chambon and colleagues (2011) who found that during dynamic social perception SCZ patients have less facilitation of performance by prior expectations.

During perception of emotions congruent with prior expectations, patients with SCZ had decreased activity in right IFG and inferior parietal lobule; regions with roles in the reinforcement of prior expectations (Summerfield and Koechlin, 2008), inhibitory control (Aron et al., 2004; Forstmann et al., 2008) and evaluation of prior expectations (Corbetta et al., 2008; O'Connor et al., 2010). The attenuation in these brain regions in SCZ may result in difficulty evaluating and forming emotion-related prior expectations (Adams et al., 2016). Furthermore, our results show that the rAMY network, functionally connecting to thalamus and parietal regions, was recruited *only* by HCs and activity in this network was correlated with faster response times for *congruent* emotions. The rAMY is a region consistently implicated in filtering noise and rapid directing of attention towards important information (such as emotional

cues) (Garvert et al., 2014; Pessoa and Adolphs, 2010). Finally, we found that SCZ total negative symptom score was associated with greater left insula activity during *congruent* conditions. Negative symptoms in SCZ have previously been linked with deficits in emotion perception (Ventura, Wood, & Hellemann, 2011) and anticipation (expectation) of emotion (Moran & Kring, 2018). Moreover, left insula hyperactivity in SCZ during emotion processing has been reported in a meta-analysis (Li, Chan, McAlonan, & Gong, 2010), with the authors arguing that hyperactivity may be due to higher sensitivity in SCZ to emotional stimuli. The finding of hyperactivity in the left insula during emotions *congruent with expectations* may imply that SCZ individuals with more negative symptoms have greater sensitivity to emotional stimuli, possibly due to deficits in emotion anticipation and less regulation by priors.

Overall our findings are in line with Chambon and colleagues (2011), such that in social contexts patients with schizophrenia have weak priors, related to greater negative symptoms. Importantly Chambon and colleagues (2011) found a dissociation between social and non-social priors, finding that in non-social contexts patient had stronger priors, related to positive symptoms. This continues a line of research showing that positive symptoms, such as hallucinations, are related to stronger prior expectations in *non-social* auditory and visual tasks (Alderson-Day et al., 2017; Powers et al., 2017; Teufel et al., 2015). Stratifying schizophrenia patients according to their symptom profile (e.g. anhedonia and social withdrawal) may provide further insight into the specific nature of prior expectancy across both social and non-social domains. Studying schizophrenia at a more refined symptom based level will undoubtedly improve our understanding of such a heterogeneous disease and the specific relationship between cognition and clinical presentation.

5.1. Conclusion

The current study provides novel insights to our understanding about the influence of prior expectations on dynamic emotion perception in SCZ. Our results indicate that in a dynamic environment, individuals with SCZ may have aberrant prior expectations, resulting in impaired perception of emotion. The related aberrant neural circuitry in SCZ involves inferior frontoparietal regions, left insula and rAMY functional network. The results from the current study further our understanding of the underlying cognitive and neural processing differences during emotion perception in patients with SCZ, which has the potential to better inform novel treatments, such as neurofeedback coupled with cognitive remediation, allowing for a more targeted intervention.

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Contributors

Author ID designed the paradigm, analysed the data and wrote the first draft of the manuscript. All authors assisted in the design of the paradigm and contributed to and have approved the final manuscript.

Conflict of Interest

The authors declare no competing financial interests.

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References

Adams, R.A., Huys, Q.J., Roiser, J.P., 2016. Computational Psychiatry: towards a mathematically informed understanding of mental illness. J Neurol Neurosurg Psychiatry 87(1), 53-63.

Alderson-Day, B., Lima, C.F., Evans, S., Krishnan, S., Shanmugalingam, P., Fernyhough, C., Scott, S.K., 2017. Distinct processing of ambiguous speech in people with non-clinical auditory verbal hallucinations. Brain 140(9), 2475-2489.

Anticevic, A., Cole, M.W., Repovs, G., Murray, J.D., Brumbaugh, M.S., Winkler, A.M., Savic, A., Krystal, J.H., Pearlson, G.D., Glahn, D.C., 2014. Characterizing Thalamo-Cortical Disturbances in Schizophrenia and Bipolar Illness. Cereb Cortex 24(12), 3116-3130.

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2004. Inhibition and the right inferior frontal cortex. Trends Cogn Sci 8(4), 170-177.

Arsalidou, M., Morris, D., Taylor, M.J., 2011. Converging Evidence for the Advantage of Dynamic Facial Expressions. Brain Topogr 24(2), 149-163.

Barbalat, G., Bazargani, N., Blakemore, S.J., 2013. The Influence of Prior Expectations on Emotional Face Perception in Adolescence. Cereb Cortex 23(7), 1542-1551.

Barbalat, G., Rouault, M., Bazargani, N., Shergill, S., Blakemore, S.J., 2012. The influence of prior expectations on facial expression discrimination in schizophrenia. Psychol Med 42(11), 2301-2311.

Bjorkquist, O.A., Olsen, E.K., Nelson, B.D., Herbener, E.S., 2016. Altered amygdala-prefrontal connectivity during emotion perception in schizophrenia. Schizophr Res 175(1-3), 35-41.

Brown, E.C., Brune, M., 2012. The role of prediction in social neuroscience. Front Hum Neurosci 6.

Chambon, V., Pacherie, E., Barbalat, G., Jacquet, P., Franck, N., Farrer, C., 2011. Mentalizing under influence: abnormal dependence on prior expectations in patients with schizophrenia. Brain 134(Pt 12), 3728-3741.

Chan, R.C.K., Li, H.J., Cheung, E.F.C., Gong, Q.Y., 2010. Impaired facial emotion perception in schizophrenia: A meta-analysis. Psychiat Res 178(2), 381-390.

Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: From environment to theory of mind. Neuron 58(3), 306-324.

Das, P., Kemp, A.H., Flynn, G., Harris, A.W.F., Liddell, B.J., Whitford, T.J., Peduto, A., Gordon, E., Williams, L.M., 2007. Functional disconnections in the direct and indirect amygdala pathways for fear processing in schizophrenia. Schizophr Res 90(1-3), 284-294.

Dieguez-Risco, T., Aguado, L., Albert, J., Hinojosa, J.A., 2015. Judging emotional congruency: Explicit attention to situational context modulates processing of facial expressions of emotion. Biol Psychol 112, 27-38.

Dima, D., Dietrich, D.E., Dillo, W., Emrich, H.M., 2010. Impaired top-down processes in schizophrenia: a DCM study of ERPs. Neuroimage 52(3), 824-832.

Diwadkar, V.A., Flaugher, B., Jones, T., Zalanyi, L., Ujfalussy, B., Keshavan, M.S., Erdi, P., 2008. Impaired associative learning in schizophrenia: behavioral and computational studies. Cogn Neurodyn 2(3), 207-219.

Dudley, R., Taylor, P., Wickham, S., Hutton, P., 2016. Psychosis, Delusions and the "Jumping to Conclusions" Reasoning Bias: A Systematic Review and Meta-analysis. Schizophr Bull 42(3), 652-665.

Dzafic, I., Martin, A.K., Hocking, J., Mowry, B., Burianova, H., 2016. Dynamic emotion perception and prior expectancy. Neuropsychologia 86, 131-140.

Fan, F.M., Tan, S.P., Yang, F.D., Tan, Y.L., Zhao, Y.L., Chen, N., Li, B.B., Song, C.S., Wang, Y.H., Jin, Z., Zhou, D.F., Milham, M.P., Zou, Y.Z., Zuo, X.N., 2013. Ventral medial prefrontal functional connectivity and emotion regulation in chronic schizophrenia: A pilot study. Neuroscience bulletin 29(1), 59-74.

Feingold, D., Hasson-Ohayon, I., Laukka, P., Vishne, T., Dembinsky, Y., Kravets, S., 2016. Emotion recognition deficits among persons with schizophrenia: Beyond stimulus complexity level and presentation modality. Psychiat Res 240, 60-65.

Forstmann, B.U., Jahfari, S., Scholte, H.S., Wolfensteller, U., van den Wildenberg, W.P.M., Ridderinkhof, K.R., 2008. Function and structure of the right inferior frontal cortex predict individual differences in response inhibition: A model-based approach. J Neurosci 28(39), 9790-9796.

Friston, K., Kiebel, S., 2009. Predictive coding under the free-energy principle. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 364(1521), 1211-1221.

Friston, K., Kilner, J., Harrison, L., 2006. A free energy principle for the brain. Journal of physiology, Paris 100(1-3), 70-87.

Friston, K.J., 2003. Statistical parametric mapping, Neuroscience Databases. Springer, pp. 237-250.

Garvert, M.M., Friston, K.J., Dolan, R.J., Garrido, M.I., 2014. Subcortical amygdala pathways enable rapid face processing. Neuroimage 102 Pt 2, 309-316.

Green, M.F., Nuechterlein, K.H., Gold, J.M., Barch, D.M., Cohen, J., Essock, S., Fenton, W.S., Frese, F., Goldberg, T.E., Heaton, R.K., Keefe, R.S.E., Kern, R.S., Kraemer, H., Stover, E., Weinberger, D.R., Zalcman, S., Marder, S.R., 2004. Approaching a consensus cognitive battery for clinical trials in schizophrenia: the NIMH-MATRICS conference to select cognitive domains and test criteria. Biol Psychiat 56(5), 301-307.

Hargreaves, A., Mothersill, O., Anderson, M., Lawless, S., Corvin, A., Donohoe, G., 2016. Detecting facial emotion recognition deficits in schizophrenia using dynamic stimuli of varying intensities. Neurosci Lett 633, 47-54.

He, Z., Deng, W., Li, M., Chen, Z., Jiang, L., Wang, Q., Huang, C., Collier, D.A., Gong, Q., Ma, X., Zhang, N., Li, T., 2013. Aberrant intrinsic brain activity and cognitive deficit in first-episode treatment-naive patients with schizophrenia. Psychological medicine 43(4), 769-780.

Huang, C.L.C., Hsiao, S., Hwu, H.G., Howng, S.L., 2013. Are there differential deficits in facial emotion recognition between paranoid and non-paranoid schizophrenia? A signal detection analysis. Psychiat Res 209(3), 424-430.

Huang, X.Q., Lui, S., Deng, W., Chan, R.C.K., Wu, Q.Z., Jiang, L.J., Zhang, J.R., Jia, Z.Y., Li, F., Li, X.L., Chen, L., Li, T., Gong, Q.Y., 2010. Localization of cerebral functional deficits in treatment-naive, first-episode schizophrenia using resting-state fMRI. Neuroimage 49(4), 2901-2906.

Irani, F., Seligman, S., Kamath, V., Kohler, C., Gur, R.C., 2012. A meta-analysis of emotion perception and functional outcomes in schizophrenia. Schizophr Res 137(1-3), 203-211.

Johnston, P.J., Enticott, P.G., Mayes, A.K., Hoy, K.E., Herring, S.E., Fitzgerald, P.B., 2010. Symptom Correlates of Static and Dynamic Facial Affect Processing in Schizophrenia: Evidence of a Double Dissociation? Schizophrenia Bull 36(4), 680-687.

Kruck, C.L., Roth, R.M., Kumbhani, S.R., Garlinghouse, M.A., Flashman, L.A., McAllister, T.W., 2011. Inferential-reasoning impairment in schizophrenia-spectrum disorders. The Journal of neuropsychiatry and clinical neurosciences 23(2), 211-214.

Leckman, J.F., Sholomskas, D., Thompson, D., Belanger, A., Weissman, M.M., 1982. Best estimate of lifetime psychiatric diagnosis: a methodological study. Arch Gen Psychiat 39(8), 879-883.

Li, H., Chan, R.C., McAlonan, G.M., Gong, Q.Y., 2010. Facial emotion processing in schizophrenia: a meta-analysis of functional neuroimaging data. Schizophr Bull 36(5), 1029-1039.

Maxwell, M.E., 1992. Manual for the FIGS. Bethesda (MD): Clinical Neurogenetics Branch, National Institute of Mental Health.

McIntosh, A.R., Bookstein, F.L., Haxby, J.V., Grady, C.L., 1996. Spatial pattern analysis of functional brain images using partial least squares. NeuroImage 3(3 Pt 1), 143-157.

Moran, E.K., Kring, A.M., 2018. Anticipatory Emotion in Schizophrenia. Clin Psychol Sci 6(1), 63-75.

Mukherjee, P., Whalley, H.C., McKirdy, J.W., McIntosh, A.M., Johnstone, E.C., Lawrie, S.M., Hall, J., 2012. Lower effective connectivity between amygdala and parietal regions in response to fearful faces in schizophrenia. Schizophr Res 134(2-3), 118-124.

Nurnberger, J.I., Blehar, M.C., Kaufmann, C.A., York-Cooler, C., Simpson, S.G., Harkavy-Friedman, J., Severe, J.B., Malaspina, D., Reich, T., 1994. Diagnostic interview for genetic studies: rationale, unique features, and training. Arch Gen Psychiat 51(11), 849-859.

O'Connor, A.R., Han, S., Dobbins, I.G., 2010. The Inferior Parietal Lobule and Recognition Memory: Expectancy Violation or Successful Retrieval? J Neurosci 30(8), 2924-2934.

Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat Rev Neurosci 11(11), 773-782.

Pinkham, A.E., Sasson, N.J., Kelsven, S., Simpson, C.E., Healey, K., Kohler, C., 2014. An intact threat superiority effect for nonsocial but not social stimuli in schizophrenia. J Abnorm Psychol 123(1), 168.

Powers, A.R., Mathys, C., Corlett, P.R., 2017. Pavlovian conditioning-induced hallucinations result from overweighting of perceptual priors. Science 357(6351), 596-600.

Robins, D.L., Hunyadi, E., Schultz, R.T., 2009. Superior temporal activation in response to dynamic audio-visual emotional cues. Brain Cognition 69(2), 269-278.

Said, C.P., Moore, C.D., Engell, A.D., Todorov, A., Haxby, J.V., 2010. Distributed representations of dynamic facial expressions in the superior temporal sulcus. J Vision 10(5).

Sheehan, D.V., Lecrubier, Y., Sheehan, K.H., Janavs, J., Weiller, E., Keskiner, A., Schinka, J., Knapp, E., Sheehan, M.F., Dunbar, G.C., 1997. The validity of the Mini International Neuropsychiatric Interview (MINI) according to the SCID-P and its reliability. Eur Psychiat 12(5), 232-241.

Summerfield, C., Koechlin, E., 2008. A neural representation of prior information during perceptual inference. Neuron 59(2), 336-347.

Teufel, C., Subramaniam, N., Dobler, V., Perez, J., Finnemann, J., Mehta, P.R., Goodyer, I.M., Fletcher, P.C., 2015. Shift toward prior knowledge confers a perceptual advantage in early psychosis and psychosis-prone healthy individuals. Proc Natl Acad Sci U S A 112(43), 13401-13406.

Underwood, R., Peters, E., Kumari, V., 2015. Psychobiology of threat appraisal in the context of psychotic experiences: A selective review. Eur Psychiat 30(7), 817-829.

Ventura, J., Wood, R.C., Hellemann, G.S., 2011. Symptom domains and neurocognitive functioning can help differentiate social cognitive processes in schizophrenia: a meta-analysis. Schizophrenia Bull 39(1), 102-111.

Figure Captions

Figure 1. Behavioural results from schizophrenia patients and healthy controls during dynamic emotion perception. A) Significant interaction, mean accuracy percentage for condition (congruent and incongruent) and group (schizophrenia and healthy controls). B) Significant main effect of group, mean missed trials for condition (congruent and incongruent) and group (schizophrenia and healthy controls). C) Significant main effect of group, discriminability index (d') for emotion videos: angry, happy, and neutral. *$p < 0.05$; **$p < 0.001$.

Figure 2. Brain activity differences between schizophrenia patients and healthy controls during dynamic emotion perception. A) Activity differences during perception of emotion incongruent with prior expectations, B) Activity differences during perception of emotion congruent with prior expectations. Warm colours indicate schizophrenia patients > healthy controls, and cool colours indicate healthy controls > schizophrenia patients. Voxel-level threshold was set at $p < 0.05$ family-wise error (FWE) corrected. C) Multiple regression analysis shows that an increase in SANS scores significantly predicted an increase in brain activity in the left insula during congruent videos. Cluster-level $p < 0.05$ family-wise error (FWE) corrected.

Figure 3. Functional connections with rAMY/behaviour PLS results for schizophrenia patients and healthy controls during dynamic emotion perception. (Left panel) A pattern of correlated whole-brain activity. (Right panel) Correlations between activity in rAMY seed and scores represent activity in the regions displayed in the left panel. Results indicate that healthy controls have differentiated rAMY functional connectivity for congruent and incongruent conditions, associated with faster response speed. Conversely, schizophrenia

patients show rAMY functional connectivity only for incongruent conditions, associated with faster response speed. Asterisks denote significant correlations based on 95% confidence intervals calculated from the bootstrap procedure.

TABLE 1

Demographic Information

	SCZ (*SD*)	HC (*SD*)	*t*/$\chi 2$	*p*-value
Mean Age (*N* = 16/16)	45.94 (9.30)	45.19 (7.93)	0.25	0.81
Gender (M : F)	9 : 7	9 : 7	0	1.0
Mean Education (*N* = 16/16)	11.69 (1.54)	15.88 (3.3)	-4.6	<0.001
Full Scale IQ (*N* = 16/16)	94.19 (12.35)	116.63 (10.92)	-5.44	<0.001
Positive and Negative Symptoms (*N* = 16)	Count	Mean (SD)		
SANS	13	1.88(1.54)		
SAPS	10	1.56(1.93)		
Affective Flattening	13	1.44(1.03)		
Alogia	3	0.25(0.58)		
Avolition	2	0.13(0.34)		
Asociality	1	0.06(0.25)		
Attention	0	/		
Hallucinations	5	0.63(1.025)		
Delusions	7	0.75(1)		
Bizarre Behaviour	1	0.13(0.5)		
Thought Disorder	1	0.063(0.25)		
Medication (*N* = 15)	Total			
Typical antipsychotic	1	-	-	-
Atypical antipsychotic	19	-	-	-
Antidepressant	6	-	-	-
Stimulant	0	-	-	-
Mood stabilizer	4	-	-	-
Sedative/hypnotic	2	-	-	-

$\chi 2$ value derived from Pearson's chi-squared test with variables group and gender.
Abbreviations: SD = standard deviation; N = sample size; M = male; F = female; SCZ = schizophrenia; HC = healthy controls; SAPS = Scale for the Assessment of Positive Symptoms (Global rating); SANS = Scale for the Assessment of Negative Symptoms (Global rating).

TABLE 2

Regional activity during emotion perception

Brain region	Hem	BA	MNI coordinates			Cluster size	T	Z
			x	y	z			
Congruent, HC > SCZ								
Inferior Frontal	R	9	60	12	22	21	6.51	5.60
Superior Temporal	B	22	62	-26	8	1433	9.62	7.39
			-56	-14	0	728	7.29	6.10
IPL	B	40	-36	-26	58	450	6.56	5.64
			46	-28	48	228	6.37	5.51
Congruent, SCZ > HC								
Lingual	L	18	-20	-74	-10	228	6.37	5.51
Cuneus	L	19	-18	-90	32	55	6.17	5.38
Incongruent, HC > SCZ								
Claustrum	R		34	0	12	29	6.11	5.33
Globus Pallidus	R		24	2	-8	14	5.56	4.95
Superior Temporal	B	41, 22	62	-26	8	2161	15.87	Inf
			-56	-12	2	1812	11.48	Inf
Incongruent, SCZ > HC								
SPL	R	7	30	-58	54	70	7.12	6.00
Precuneus	R	7	10	-78	48	41	6.74	5.75
Fusiform	L	19	-22	-74	-12	5153	11.68	Inf
		37	-44	-58	-8	24	6.03	5.28
Multiple Regression: SANS during Congruent								
Insula	L	13	-48	16	2	211	9.74	4.9

Abbreviations: Hem = hemisphere; BA = Brodmann area; R = right; L = left; B = bilateral; IPL = inferior parietal lobule; SPL = superior parietal lobule; HC = healthy controls; SCZ = schizophrenia; SANS = Scale for the Assessment of Negative Symptoms. All reported activations for the full factorial are peak-level $p < 0.05$ FWE corrected. The reported activation for the multiple regression is cluster-level $p < 0.05$ FWE corrected.

TABLE 3
Functional connections with right amygdala during emotion perception

Brain region	Hem	BA	MNI coordinates			Voxels	BSR
			x	y	z		
rAMY network for HC during congruent conditions (not in SCZ)							
Cingulate	R	32, 23	18	26	28	158	4.25
Precuneus	L	31, 7	-10	-56	38	134	5.16
TPJ	L	39	-36	-58	28	250	3.95
Paracentral Lobule	L	5	0	-42	68	105	3.66
Thalamus	R		2	-6	0	56	5.17
Caudate Tail	R		30	-44	16	125	4.17
rAMY network for HC and SCZ during incongruent conditions							
dlPFC	B	10, 8, 9, 6	34	60	10	17783	8.39
			-20	56	12	120	4.80
Precentral	B	6, 44	38	-2	32	720	7.13
vlPFC	B	45, 47, 46	-48	24	14	380	5.02
			52	36	2	114	4.11
Middle Frontal	B	9, 6, 46, 10	-34	22	26	204	5.10
dmPFC	R	8	12	42	32	133	4.91
Paracentral Lobule	B	5	6	-24	56	380	4.44
Superior Frontal	R	6	4	6	68	452	4.33
vmPFC	R	11	4	36	-22	114	3.36
Parahippocampal	B	27, 34, 30	20	-38	-2	140	5.75
			-22	2	-16	764	5.06
Posterior Cingulate	B	30	24	-62	8	914	5.70
Anterior Cingulate	B	32, 24, 10	-24	40	4	1253	5.53
			4	22	18	113	5.35
Hippocampus	L		-34	-36	-8	445	4.46
SN	B		-6	-14	-8	1577	6.36
			16	-14	-10	206	5.66
Red Nucleus	L		-2	-18	-12	132	5.09
Precuneus	B	31	-28	-70	28	26798	8.75
Cuneus	B	17, 19, 18	-18	-90	12	8799	6.91
			6	-84	38	149	3.80
Lingual	B	19, 17, 18	-34	-66	4	137	6.82
			28	-66	6	237	4.73
Middle Occipital	B	18	-24	-90	20	446	5.73
			32	-88	8	121	4.98
Inferior Occipital	B	18, 19	-26	-94	0	158	4.42
IPL	B	40	44	-34	38	5292	7.83
			-48	-30	28	2134	6.99
Postcentral	B	3, 5, 40	-58	-16	42	5480	6.34
			24	-34	74	685	5.76

TPJ	B	39, 40	-28	-58	42	691	6.23
			58	-38	36	2511	5.76
SPL	L	7	-24	-64	54	532	5.56
Precuneus	R	7	26	-74	44	149	4.01
Anterior Nucleus	R		14	0	2	3350	6.69
Putamen	B		22	2	2	3304	6.21
			-26	16	2	463	4.26
Claustrum	B		36	14	-6	2588	6.13
			-34	14	-6	1975	6.13
Insula	B	13	-30	-36	24	102	5.09
			34	6	20	104	4.04
Thalamus	B		-4	-14	-6	331	5.01
			12	-24	18	105	3.89
Superior Temporal	B	22, 41, 13	-58	-56	24	153	6.61
			46	-36	4	963	6.13
Middle Temporal	B	21, 37, 39	56	-44	8	1708	6.35
			-44	-56	6	887	5.69
Inferior Temporal	L	21	-64	-16	-20	180	4.93

Abbreviations: Hem = hemisphere; BA = Brodmann area; R = right; L = left; B = bilateral; BSR = bootstrap ratio; voxels = number of voxels (one voxel volume=6 mm3); rAMY = right amygdala; dlPFC = dorsolateral prefrontal cortex; vlPFC = ventrolateral prefrontal cortex; vmPFC = ventromedial prefrontal cortex; SN = Subthalamic Nucleus; IPL = inferior parietal lobule; TPJ = temporoparietal junction; SPL = superior parietal lobule. All reported activations are ≥100 voxels.