Title: Schizotypy and mentalizing: an fMRI study

Authors: Acosta H*[a,b], Straube B[a], Kircher T[a]

Affiliations:

[a] Department of Psychiatry and Psychotherapy, Philipps-University of Marburg

[b] The FinnBrain Birth Cohort Study, Turku Brain and Mind Center, Department of Clinical Medicine, University of Turku, Finland

Author's address: Department of Psychiatry and Psychotherapy, Philipps-University of Marburg, Rudolf-Bultmann St 8, 35039 Marburg, Germany, Tel.:+49 6421 58 66429, Fax: +49 6421 58 68939, Email: schneid5@staff.uni-marburg.de

Abstract

Introduction: Schizotypy is a personality trait characterized by subclinical schizophrenia symptoms. Individuals with schizophrenia typically display behavioral mentalizing deficits and altered neural correlates during mentalizing. While schizotypy has been inconsistently related to behavioral mentalizing skills, its neural correlates of mentalizing are understudied so far. With this study we tested the association between schizotypy traits in healthy subjects and mentalizing-related neural correlates to provide new insights into neural processes associated with subclinical schizophrenia traits.

Methods: Brain activation was measured using fMRI during an interactive mentalizing paradigm (Prisoner's Dilemma Game) in 164 healthy subjects. The Schizotypal Personality Questionnaire (SPQ-B) was administered to assess the three dimensions of schizotypy, i.e., cognitive-perceptual, interpersonal and disorganized.

Results: We found that interpersonal schizotypy was significantly negatively correlated with brain activation in bilateral precunei and right caudate nucleus (among others) during mentalizing. By contrast, disorganized schizotypy was significantly positively correlated with mentalizing-associated neural activation in right precuneus, left middle cingulate cortex and right cerebellar hemisphere. No significant associations for cognitive-perceptual schizotypy and the SPQ-B total score were found.

Discussion: Our study showed that interpersonal and disorganized schizotypy are associated with neural correlates of mentalizing in brain regions that are involved in self-processing and mentalizing. These brain regions have also been linked to mentalizing in schizophrenia.

Keywords: Theory-of-mind; self-processing; schizophrenia; precuneus; cooperativity

1. Introduction

According to the dimensional perspective of mental disorders, subclinical schizophrenia symptoms are traceable in the general population in the form of schizotypy, ranging along a continuum from a mentally healthy condition to potential dysfunction and psychosis (Ettinger et al., 2015; Modenato & Draganski, 2015; M. T. Nelson, Seal, Pantelis, & Phillips, 2013). The high end of this continuum represents schizophrenia and schizophrenia spectrum disorders (M. T. Nelson et al., 2013). High schizotypy is often related to lower life quality, addiction problems, and lower social, academic, and occupational levels of functioning (Ettinger et al., 2015).

Both schizophrenia and schizotypy share a three factor structure of symptoms (Cohen, Mohr, Ettinger, Chan, & Park, 2015; Ettinger, Meyhoefer, Steffens, Wagner, & Koutsouleris, 2014). The cognitive-perceptual (or positive) dimension of schizotypy refers to perceptual alterations and unusual thoughts that resemble the positive symptoms in schizophrenia (e.g., delusions and hallucinations). The interpersonal (or negative) dimension of schizotypy is characterized by social anhedonia, reduced positive affect and volition, and high negative affect, similarly to the apathy, amotivation and alogia observed as negative symptoms in schizophrenia. The third, disorganized dimension of schizotypy describes eccentric behavior and formal thought disorder comparable to the disorganized symptoms in schizophrenia (Cohen et al., 2015; Ettinger et al., 2014). The three schizotypal dimensions are linked to distinct behavioral, (socio)cognitive, emotional and neurobiological correlates (Cohen et al., 2015). Individual differences in schizotypy show temporal stability and can be reliably assessed in clinical interviews and/or by use of self-report measures (Ettinger et al., 2014). Frequently administered self-report measures are the Schizotypal Personality Questionnaire (Raine, 1991; Raine et al., 1994) and its brief version (SPQ-B) (Raine & Benishay, 1995).

Mentalizing, also called theory-of-mind, is a core sociocognitive ability defined by “imputing mental states to oneself and others” (Premack & Woodruff, 1978). Mentalizing provides humans with “the ability to predict and explain people's behavior with reference to mental states” (Repacholi & Slaughter, 2003). A mentalizing-related neural network has been characterized in a meta-analyis by Mar (Mar, 2011): This network comprises the bilateral medial and inferior prefrontal cortices, temporoparietal junctions (TPJs), superior temporal sulci, temporal poles, posterior cingulate cortices, precunei, and possibly the amygdala.

The behavioral performance in mentalizing tasks is significantly impaired in patients with schizophrenia compared to controls as shown in several meta-analyses (Bora, Yucel, & Pantelis, 2009; Savla, Vella, Armstrong, Penn, & Twamley, 2013; Sprong, Schothorst, Vos, Hox, & van Engeland, 2007). Several neuroimaging studies reported alterations of mentalizing-related brain activation in schizophrenia patients compared to controls (for a review see (Bosia, Riccaboni, & Poletti, 2012). Behavioral studies investigating the association between schizotypy and mentalizing yielded mixed results. Total schizotypy has been related to poorer mentalizing performance in some studies (Henry, Bailey, & Rendell, 2008; Langdon & Coltheart, 1999; Morrison, Brown, & Cohen, 2013), but not in others (Barragan, Laurens, Navarro, & Obiols, 2011; Fernyhough, Jones, Whittle, Waterhouse, & Bentall, 2008; Jahshan & Sergi, 2007; Pickup, 2006). One study found that affective, but not cognitive mentalizing was impaired in individuals with elevated schizotypy (Kocsis-Bogár, Kotulla, Maier, Voracek, & Hennig-Fast, 2017). Some studies that differentiated between positive and negative schizotypy reported either insignificant results for both schizotypy dimensions (Fernyhough et al., 2008), positive associations for both dimensions (Henry et al., 2008) or significant associations for positive, but not negative schizotypy (Barragan et al., 2011; Gooding & Pflum, 2011; Pickup, 2006). One study yielded inconsistent results: Negative, but not positive schizotypy was associated with less mentalizing capacity in the first experiment, while in the second experiment poor mentalizing was related to disorganized and positive schizotypy, but not negative schizotypy (Langdon & Coltheart, 1999). Further, in one study positive schizotypy symptoms (i.e., delusional thinking) correlated with over-mentalizing (i.e., “inferring mental states when none are obviously suggested”) (Fyfe, Williams, Mason, & Pickup, 2008). Similarly to schizophrenia, the association between schizotypy and mentalizing remained significant when neurocognitive skills (e.g., executive functions) were controlled for (Kocsis-Bogár et al., 2017; Pickup, 2006). In sum, the association between schizotypy and behavioral measures is mostly weak and inconsistent. It has been proposed that “compensatory mechanisms may be mitigating social cognitive performance in those with elevated schizotypy who may be using alternative strategies to solve daily social cognitive challenges“ (Cohen et al., 2015).

The analysis of neural correlates of mentalizing is a further promising step in elucidating sociocognitive processing in schizotypy. However, up to date, only few studies examined the mentalizing-related neural correlates of total and positive schizotypy, and – to the best of our knowledge – none investigated the mentalizing-related neural correlates of the negative and disorganized dimensions of schizotypy. In a functional near-infrared spectroscopy study of the frontal cortex total schizotypy correlated positively with activation in the right dorsomedial frontal cortex during the “Reading the Mind in the Eyes” task (Platek et al., 2005). In two fMRI studies high compared to low positive schizotypy was associated with higher mentalizing-related activation in frontal gyri: In a Cartoon task the bilateral middle and inferior frontal gyri and right superior frontal gyrus were higher activated (Modinos, Renken, Shamay-Tsoory, Ormel, & Aleman, 2010), and during movies requiring explicit false belief reasoning the left inferior frontal gyrus was higher activated in high compared to low positive schizotypy (van der Meer, Groenewold, Pijnenborg, &

Aleman, 2013). Interestingly, no behavioral differences in mentalizing performance were observed in either fMRI study supporting the notion that individuals with elevated schizotypy might use compensatory neural activations during sociocognitive processing.

In our study we investigated for the first time the association between the three schizotypy dimensions and mentalizing-related neural correlates. We applied the iterative Prisoner's Dilemma Game (PDG) as mentalizing task. This nonstory-based task has been successfully employed in several neuroimaging studies of our group and others (Kircher et al., 2009; Rilling et al., 2012; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b; Schneider-Hassloff, Straube, Nuscheler, Wemken, & Kircher, 2015). Nonstory-based tasks compared to story-based tasks demand less executive and language processing which are not necessarily linked to the mentalizing process itself (Apperly, Samson, Chiavarino, & Humphreys, 2004). Several types of nonstory-based tasks have been applied, such as cartoon sequencing (Brüne, 2005a), animated shapes (Castelli, Happé, Frith, & Frith, 2013), and video clips of social interactions (Dziobek et al., 2006), of false-belief scenes (Bardi, Desmet, Nijhof, Wiersema, & Brass, 2017) or of strange stories (Murray et al., 2017). Most of these tasks require an explicit use of mentalizing (i.e., “offline” mentalizing) to answer questions after each video clip about the agent’s thoughts. However, real-life social situations usually require implicit, “online” mentalizing (Chan & Chen, 2011). It has been put forward that the explicit, “offline” laboratory tasks cannot adequately model the mentalizing demands of real-life social interactions and might fail to detect the difficulties that persons with psychiatric disorders face in daily life (Brüne, 2005b; Chan & Chen, 2011). Recently, video clips of false-belief scenes have been adapted for the implicit detection of mentalizing (Bardi et al., 2017; Kovács, Kühn, Gergely, Csibra, & Brass, 2014; Naughtin et al., 2017). Nevertheless, the aforementioned tasks mostly focus on the third-person perspective, i.e., subjects are not socially interacting, and during the tasks no direct feedback on the subject's behavioral choices is provided. This remarkably differs from daily life contexts where one has to consider the impact of one's own choices on the interaction partner (Chan & Chen, 2011). Conversely, interactive games are expected to "model a real-life social situation" (Rilling et al., 2012) involving the subject in a social interaction (i.e., adding a first-person perspective), eliciting implicit "online" mentalizing and providing feedback on the subject's decisions. The PDG has been widely used in social research to investigate reciprocal cooperation and altruism versus selfish and defective behavior. During the PDG the participants have to consecutively make a decision to either cooperate or defect with their game partner. The game outcome depends on the decisions of both players. The task evokes inferences about the other's intentions and beliefs; it thereby allows for the implicit detection of mentalizing which is regarded ~~processes~~ as the key mechanism to monitor both cooperative and defective strategies (Chan & Chen, 2011). In addition, reciprocated versus unreciprocated cooperation in the PDG game ~~was~~ has been shown to be associated with higher activation of striatal parts of the mesolimbic dopamine system (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a). Attenuated striatal prediction error signaling has been observed in patients with schizophrenia (Morris et al., 2012) and individuals with elevated schizotypy (Corlett & Fletcher, 2012). However, to date, the PDG has rarely been applied in schizophrenia research, even though interactive "online" mentalizing tasks have been regarded as a promising tool for probing mentalizing capacities in persons with psychiatric disorders (Brüne, 2005b; Chan & Chen, 2011). So far, one behavioral study reported a negative correlation between mentalizing measures in the PDG and the severity of delusions of reference (Chan et al., 2010). Recently, a neuroimaging study observed a lower functional connectivity between right temporoparietal junction and temporal lobe areas in patients with schizophrenia compared to controls during a PDG (Bitsch, Berger, Nagels, Falkenberg, & Straube, 2018a).

We hypothesized that schizotypy is associated with altered activation in the neural mentalizing network during the PDG. We expected a significant relation between positive schizotypy and mentalizing-related neural activation in frontal brain areas (e.g., in middle, inferior and superior frontal gyri) comparable to Modinos (Modinos et al., 2010) and van der Meer (van der Meer et al., 2013). We hypothesized that negative and disorganized schizotypy are correlated with distinct alterations of mentalizing-associated neural activations (e.g., in frontal and parieto-temporal brain areas) (see Cohen et al., 2015). Additionally, we explored whether the schizotypy dimensions are associated with variations in playing behavior and with distinct neural activation (especially in striatal regions) depending on the co-player's reciprocity of cooperative or defective behavior.

2. Methods

2.1 Participants

In total, data from 164 healthy subjects (78 female = 47.6%; mean age = 23.97 years, SD= 3.09, range 19-35) were used for the analysis. All participants were students of the universities of Marburg or Gießen, Germany. Inclusion criteria were age (18–40 years), right-handedness (as assessed by the Edinburgh Inventory, Oldfield, 1971, inclusion criterion > +40), German as native tongue, and Western- or Middle-European descent. Exclusion criteria were history of major psychiatric disorders of participants and their first-degree relatives according to ICD-10 (using the Mini-International Neuropsychiatric Interview, Ackenheil, Stotz, Dietz-Bauer, & Vossen, 1999, relevant medical or neurological diseases, psychology students, and metal implants or other MRI contraindications. Participants gave written informed consent and the study protocol was approved by the local ethics committee according to the declaration of Helsinki.

2.2 Measures and Procedure

2.2.1 Schizotypy

Individual schizotypy was assessed by use of a German version of the Schizotypal Personality Questionnaire – Brief (SPQ-B) (Klein, Andresen, & Jahn, 1997; Raine & Benishay, 1995). This self-report measure contains three subscales: the cognitive-perceptual (positive) schizotypy dimension (8 items), the interpersonal (negative) schizotypy dimension (8 items) and the disorganized schizotypy dimension (6 items). Each item has to be answered with “Yes” or “No”. The total sum score of schizotypy (22 items) ranges from 0 to 22 and the total mean score from 0 to 1.

The questionnaire was administered prior to scanning (in general at least one day before). The internal consistency reliability of the subscales’ scores was assessed with the Kuder-Richardson Formula 20 (kr20): kr20(cognitive-perceptual)= 0.33, kr20(interpersonal)= 0.72, kr20(disorganized)= 0.57, kr20(total)= 0.68. Reliability values were comparable to Compton et al. (Compton, Chien, & Bollini, 2007) for the interpersonal and disorganized dimension, but lower for the cognitive-perceptual dimension and the total score.

2.2.3 FMRI Paradigm

A Prisoner's Dilemma Game was constructed using a modified version of a published task of our and other groups (Krach et al., 2008; Rilling et al., 2004b). In this game two players are simultaneously faced with the decision to press the right or left button. Depending on the decision of both players both gain a certain amount of points according to the decision matrix: If both players choose the left button, each one gains 20 points. If both players press the right button, each one receives zero points. If one player has chosen the right button and the other one the left button, the right button press wins 20 points, the left button press 10 points (Figure SI-1). Participants were instructed with two conflicting goals, “win the series of games and reach as many points as possible”. As these goals could not be accomplished by choosing always the same button, the decision matrix was designed to ensure a variable pressing of both buttons and an implicit use of mentalizing (Krach et al., 2008). In the control condition participants had to press one of the buttons without facing any consequences of the choice. The control condition therefore did not entail mentalizing.

Prior to scanning the subjects received a comprehensive instruction and practiced the game 15 trials at minimum to become familiarized with the game rules and the decision matrix. Participants were told that they would play an online game in order to examine social decision making and that they would play consecutively against two different, but same-sex co-players who differ in their problem solving style and whom the participants would not meet to avoid any bias by personal contact. In reality, participants played against a computer. In a between-group design (3 groups) we provided an additional description of one of the co-player’s problem solving style (‘modestly efficient and rather reserved’ vs. ‘modestly efficient and rather good-natured’) for two of the groups. In the analyses we collapsed all groups (as they were not relevant for the current analyses) and controlled for the between-group design (see 2.3.2). The fMRI paradigm was performed using Presentation software (Version 14.1, Neurobehavioral Systems, San Francisco, CA). At the beginning of the game session in the scanner, a summary of the instructions was presented to the participants. To enhance the credibility of the co-players' existence the information was given that the game starts when every player is ready. Each player's readiness for action was indicated by a green tick on a slide. On the first slide only two of the three players were ticked off. After a short waiting period the next slide showed that all three players were ready and then the game started. The fMRI paradigm lasted 15.06 min and comprised 30 blocks: 2 blocks with the first co-player were followed by one block of the control condition and then two blocks with the second co-player followed. This sequence was repeated five times, resulting in 10 blocks for control and 10 blocks for the game task with each of the two co-players, i. e. 20 in total. Each block took 27.5 s plus a variable interval (jitter; mean value 623.9 ms, range 0-1000 ms) and started with one instruction screen (3.5 s + the jitter), announcing the next condition, followed by six game trials. Each trial consisted of one crosshair and one matrix screen, each appearing for 2 seconds. The crosshair screen indicated the time for the decision / button pressing. On the matrix screen information about the buttons both players had pressed and about the scores - of the current trial and accumulated over the trials in one block - appeared. In the control condition the matrix screen contained hash signs instead of scores (Figure SI-2). After the MR scanning participants were asked to remember experimental details to control for adequate attention to the task.

2.2.4 Playing behavior

Cooperativity of playing behavior (C) was defined as quantity of left button choices. Further, we computed the ratio of the subject's cooperative versus defective behavior after each of the four possible game scores (which were mutual cooperation (CC), defection of subject (study proband) and cooperation of co-player (DC), cooperation of subject and defection of co-player (CD) and mutual defection (DD)). This resulted in following four variables: “C/D after CC”, “C/D after CD”, “C/D after DC” and “C/D after DD”.

2.2.5 FMRI data acquisition

Data were acquired on a 3 Tesla whole body scanner (Siemens MAGNETOM Trio - A Tim System, Germany) at the Department of Psychiatry, University of Marburg. Functional neuroimaging data were collected using T2*-weighted gradient echo planar imaging sequence sensitive to BOLD contrast (64 x 64 matrix size, 230 mm field of view, 30 ms echo time, 2.25 s repetition time, 90° flip angle, slices acquired in sequential (ascending) order with 20% distance factor, 36 axial slices orientated parallel to the AC-PC line covering the whole brain, slice thickness 3.6 mm, in plane resolution 3.6 mm x 3.6 mm). Four hundred functional images were collected and the onset of each block was synchronized to a scanner pulse.

2.3 fMRI data analysis

Functional images were analyzed using Statistical Parametric Mapping standard routines and templates (SPM8; http://www.fil.ion.ucl.ac.uk/spm/). After discarding the initial six images to remove the influence of T1 saturation effects, functional images were spatially realigned to correct for head motion, normalized into a standard stereotactic anatomical MNI-space (resulting voxel size 2 x 2 x 2 mm), smoothed with a 8-mm isotropic Gaussian FWHM kernel and high-pass filtered. The high-pass filter was adapted to the experimental design with a cut-off period of 342 s; one experimental cycle took about 171 s including the blocks with both co-players and the control condition resulting in six blocks with a maximum length of 28.5 s for each block.

2.3.1 Single subject (first-level) analyses

A general linear model was specified for each participant including two epoch regressors, modeling the game task (ment) and the control condition (con) (each without instruction) as well as six regressors modeling head movement parameters. The contrast for the task versus control condition (ment > con) was calculated on single subject level. Parameter estimate (β-) images were calculated for each condition and each subject.

We additionally computed a general linear model that included five epoch regressors, modeling the control condition and the four different possible game scores as separate epochs (see Rilling et al., 2012, 2004a: mutual cooperation (CC), defection of subject and cooperation of co-player (DC), cooperation of subject and defection of co-player (CD) and mutual defection (DD). The game epochs comprised the time window when the players choices were revealed and (except at the end of a block) the subsequent decision was to be made.

2.3.2 Group analyses: Mentalizing and SPQ

SPM8 group analyses were performed by entering the first-level contrasts (ment > con) of each subject into a random-effects one-sample t-test. Age and sex were entered as covariates of no interest into all models. To control for effects of the three slightly different instructions regarding the two co-players (which we applied in a between-subject design and that are of no interest here), we included two dummy-coded covariates of no interest into all group-level analyses.

In the first model the individual mean scores of the three SPQ-B subscales (cognitive-perceptual, interpersonal and disorganized) were entered as three covariates of interest to investigate the correlation between the individual SPQ-B mean scores and the mentalizing-related activity (ment > con). For illustrative purposes eigenvariates of significant clusters were extracted for each subject using the VOI function of SPM8.

In a second model, because the distribution of all three schizotypy subscales was right-skewed, we contrasted subjects with low (<= first quartile median (=Q1)) and high (>= fourth quartile median (=Q4)) scores of the three SPQ-B dimensions in exploratory factorial analyses.

Finally, in a third model, we examined the association between the three SPQ-B dimensions and the mentalizing-related neural activation for each of the possible game scores (CC, DC, CD, DD). We entered the first-level contrasts of each game epoch vs. the control condition (CC>con, DC>con, CD>con, DD>con) in a full factorial model with one four-level factor. The three SPQ-B dimension scores were entered as covariates of interest in interaction with the four conditions. We explored significant differences between the game scores for the three SPQ-B dimensions comparing the contrasts of concordantly (CC, DD) *vs.* differently (CD, DC) reciprocated game trials, separately for cooperative and competitive choices: (CC<CD), (CC>CD), (DD<DC) and (DD>DC). The compared contrast pairs were thereby also similarly frequent (see 3.2).

Additionally, we investigated the association between the total schizotypy score and mentalizing-related activity (ment > con), and we computed all three models (see above) with the total schizotypy score. Further, we explored the interaction between schizotypy dimensions comparably to Kwapil et al. (Kwapil, Gross, Silvia, & Barrantes-Vidal, 2013). We computed an interaction term for the significantly intercorrelated interpersonal and disorganized schizotypy dimensions (i.e., multiplying the mean-centered SPQ-B scores of both dimensions) and we explored its association with mentalizing-related neural activity (ment>con; CC>con, DC>con, CD>con, DD>con) in two models (with the three SPQ-B dimension scores as additional covariates).

We chose a voxel-wise threshold of P<0.001 uncorrected for multiple comparisons. Activity was cluster extent threshold corrected for multiple comparisons employing Monte-Carlo simulation (Slotnick & Schacter, 2004). Assuming an individual voxel type I error of P<0.05, a simulation with 1000 independent iterations indicated that a cluster extent of 47 contiguous resampled voxels is necessary to correct for multiple voxel comparisons at P<0.001.

Localization of activation peaks are always reported as MNI-coordinates. For the anatomical localization of the functional data, probabilistic cytoarchitectonic maps according to the SPM Anatomy Toolbox (version 2.1/ 2.2c; http://www.fz-juelich.de/inm/inm-1/DE/Forschung/_docs/SPMAnatomyToolbox/SPMAnatomyToolbox_node.html) (Eickhoff et al., 2005) and Wake Forest University

PickAtlas software (version 2.5.2; fmri.wfubmc.edu) were used as reference. Statistical analyses of the behavioral data and of the eigenvariates were performed using R 3.3.2 (http://www.r-project.org/) (R Core Team, 2016). For ANOVA analyses we applied the “Anova (lm)” function from the package “car” (Fox & Weisberg, 2011). Further packages in use were “Hmisc” (Harrell Jr., 2017), “psy” (Falissard, 2012), “nortest” (Gross & Ligges, 2015) and “psych” (Revelle, 2017).

3. Results

3.1.1 Schizotypy - descriptive information

Descriptive information for the three SPQ-B dimensions, the total schizotypy score, age and sex are presented in Table 1. The SPQ-B interpersonal dimension was moderately, but significantly correlated with the disorganized dimension. No significant correlations between the cognitive-perceptual and any other SPQ-B dimension were observed. Age was not significantly related to the SPQ-B scores, but men showed significantly higher SPQ-B scores in the disorganized dimension than women (M(men)= 0.22, M(women)= 0.13, p= 0.003).

3.1.2 Association between schizotypy and behavioral measures of PDG

The most frequent game outcome was mutual defection [(DD: M= 41.82, SD= 8.03); (DC: M= 39.43, SD= 8.74); (CD: M= 17.90, SD= 7.98); (CC: M= 20.15, SD= 8.76)]. Men showed more behavioral cooperativity (i.e., a higher frequency of pressing the left button) than women (Table 2). Schizotypy was unrelated to behavioral cooperativity (Table 2). We observed that the ratio of cooperative versus defective behavior after mutual defection (C/ D after DD) was weakly, but significantly correlated with the total (r= 0.17, p= 0.029) and the interpersonal schizotypy scores (r= 0.17, p= 0.026), even when we controlled for age and sex: The higher the schizotypy, the more cooperative the subject's behavior was after mutual defection (Table 2). However, further analyses showed that this effect was based on a single outlier (C/D after DD: SD > 8). After we removed the outlier, the correlation coefficients for (C/D after DD) were reduced to insignificance (total schizotypy: r= 0.068, p= 0.389, interpersonal schizotypy: r= 0.039, p= 0.621). Mentalizing-related activity of this subject did not relevantly deviate from the mean (< 2 SD), and the reported associations between schizotypy and mentalizing-related activity (see 3.3) remained significant if this subject was removed from analysis.

3.1.3 FMRI-analysis of mentalizing-related activity

The mentalizing-related neural activity (ment > con) was investigated in the first model. A large network was strongly activated that involved bilateral superior (medial) frontal gyri, inferior frontal gyri, hippocampi, (anterior, middle and posterior) cingulate cortices, superior and inferior parietal lobules, precunei, temporal poles, temporoparietal junctions, and on the right hemisphere middle frontal gyrus, medial orbital frontal gyrus, superior temporal gyrus, and amygdala among others. A detailed analysis and discussion has been published elsewhere (Schneider-Hassloff et al., 2015). This large network was also activated for each game score condition (CC>con, CD>con, DC>con, DD>con), as analyzed in the third model.

3.2 FMRI-analysis of the association between schizotypy and mentalizing-related activity

3.2.1 Whole sample

First, we analyzed the correlation between the three SPQ-B dimensions and mentalizing-related neural activation. Significant results are shown in Table 3. Interpersonal schizotypy was negatively related to the neural activation in bilateral precunei and olfactory cortices as well as right caudate nucleus and superior occipital gyrus. Disorganized schizotypy was positively correlated with the neural activation in right precuneus and cerebellar hemisphere, left superior parietal lobule and middle cingulate cortex, and bilateral superior occipital gyri. Interestingly, neural activation in (non-overlapping) parts of the right precuneus was related to both schizotypy dimensions, but in opposite direction. No significant associations were found for the cognitive-perceptual dimension and the total schizotypy score. Exploring the interaction of interpersonal and disorganized schizotypy we found that the interaction term negatively correlated with neural activation in right superior and middle frontal gyri (x/y/z= 20/46/36, k= 168, t= 3.73, p(FWE)= 0.611). The results for the three schizotypy dimensions were comparable to those presented in Table 3 (data not shown).

3.2.2 First and fourth quartile split

Because of the skewness of the schizotypy scores we additionally compared high and low schizotypal subjects in separate exploratory models: SPQ-B cognitive-perceptual: Q1= 0 (n= 89), Q4= 0.125 (n= 75); SPQ-B interpersonal: Q1= 0 (n= 50), Q4= 0.375 (n= 54); SPQ-B disorganized: Q1= 0 (n= 75), Q4= 0.333 (n= 46); SPQ-B total: Q1= 0.045 (n= 47), Q4= 0.273 (n= 42). Because of the skewed distribution, the first quartile split is equal to the median split in cognitive-perceptual schizotypy. Scores of the first quartile significantly differed from those of the fourth quartile for each schizotypy dimension and for the total

SPQ-B score (all p<0.001). Significant results of the exploratory models are presented in Table SI-1. They mainly support the findings from the whole brain analyses with few differences: Subjects with high compared to low disorganized schizotypy activated both right and left precunei to a higher extent and no differences were any longer observed in middle cingulate cortex and cerebellum. In addition, individuals with low compared to high total schizotypy scores activated left middle temporal gyrus to a higher extent during mentalizing.

3.3 Association between schizotypy and mentalizing-related neural activations – comparison of game scores

We explored the association between schizotypy and the mentalizing-associated neural activity separately for the four different possible game scores (CC>con, CD>con, DC>con, DD>con; see 2.3.2), in order to find out whether the association between schizotypy and mentalizing-related activity is altered during different game scores. Significant results of the association between schizotypy and the mentalizing-related activity that is specific for a game score are presented in the supplement (Table SI-2a/b). Comparing the different game outcomes (CC>CD; CC<CD; DC>DD; DC<DD), we found that interpersonal and cognitive-perceptual schizotypy, but not disorganized schizotypy, showed significantly different associations with mentalizing-related neural activity depending on the game score (Table 4). Cognitive-perceptual schizotypy was significantly more positively correlated with neural activity in left middle and superior frontal gyri as well as bilateral thalami and caudate nuclei after mutual defection compared to unreciprocated defection (DC<DD), while interpersonal schizotypy was significantly more positively related to neural activity in bilateral middle and inferior frontal gyri, middle and posterior cingulate cortices, precunei and cerebelli (among others) (contrast: DC<DD). Interpersonal schizotypy was also significantly more positively correlated with mentalizing-related activity in left middle and

anterior cingulate cortex, and in the left insular lobe when the subject's cooperative response was reciprocated with a cooperative compared to a defective response (CC>CD). Total schizotypy was significantly associated with neural activity in middle cingulate cortex for (CC>CD) and in bilateral middle and inferior frontal gyri, middle and posterior cingulate cortices, thalami, caudate nuclei, and right insular lobe and precuneus (among others) for (DC<DD) (Table SI-3). The interaction term of interpersonal and disorganized schizotypy was significantly more positively correlated with mentalizing-related neural activity in left precuneus, superior occipital gyrus and middle frontal gyrus for unreciprocated compared to mutual cooperation (CC < CD) (Table SI-4).

4. Discussion

With this study we investigated the association between schizotypy and mentalizing-related brain activation during an interactive game. Our results showed for the first time that the three schizotypy dimensions are differently related to mentalizing-associated neural activation. Higher disorganized schizotypy was associated with higher activation of right precuneus and cerebellar lobule V and VI, bilateral superior occipital gyri and left superior parietal lobule and middle cingulate cortex. By contrast, higher interpersonal schizotypy was related to lower activation of bilateral precunei and olfactory cortices, right caudate nucleus and superior occipital gyrus. No significant results were found for the cognitive-perceptual dimension and the total schizotypy score. In an exploratory analysis we observed that the interpersonal and disorganized schizotypy dimension significantly interacted on mentalizing-related neural activity in right prefrontal gyri.

Our results confirm our hypothesis that interpersonal and disorganized schizotypy are associated with distinct activations of the mentalizing-related network in parietal brain areas. Our results also provide further support that the neurobiological correlates differ between the schizotypy dimensions. Moreover, our data hint at a significant interaction between the interpersonal and disorganized schizotypy dimensions.

In our study we also explored whether the association between schizotypy and mentalizing-related activity differs between the game scores: Four different game scores were possible in our task depending on the player's (study proband) and co-player's response (CC, CD, DC, DD). We found that in individuals with higher interpersonal and cognitive-perceptual schizotypy mutual compared to unreciprocated defection was followed by a higher activation of several mentalizing-related brain areas (such as bilateral middle and inferior frontal gyri, cingulate cortices and precunei for interpersonal schizotypy and left middle and superior frontal gyri and bilateral thalami for cognitive-perceptual schizotypy). By contrast, reciprocated compared to unreciprocated cooperation elicited higher neural activation in left cingulate cortex and insula in persons with higher interpersonal schizotypy, and lower neural activation of left precuneus and middle frontal gyrus in persons with high interaction scores of interpersonal and disorganized schizotypy.

4.1 Neural correlates of mentalizing-related activity

During mentalizing, our subjects activated a large network including bilateral middle frontal gyri, cingulate cortices, precunei and temporoparietal junctions (among others). Hence our results show that relevant brain regions of the neural mentalizing network have been activated by our task, as we have shown previously (Schneider-Hassloff et al., 2015).

4.2 Schizotypy and mentalizing-related neural correlates

In our study, we found that higher disorganized schizotypy was related to the higher activation of right precuneus and cerebellar volume, bilateral superior occipital gyri and left superior parietal lobule and middle cingulate cortex. Interpersonal schizotypy was associated with lower activation of bilateral precunei and olfactory cortices, right caudate nucleus and superior occipital gyrus. Several of these regions play an important role in mentalizing, in first place the precuneus, but also the middle cingulate cortex and caudate nucleus (Abu-Akel & Shamay-Tsoory, 2011; Mar, 2011).

Disorganized and interpersonal schizotypy showed opposite activations of the precuneus during our mentalizing task. The precuneus is a major association area involved in higher order cognitive functions such as mentalizing, mental imagery, episodic memory retrieval, agency and self-processing playing a crucial role in the default mode network (Cavanna & Trimble, 2006). The precuneus is also critically involved in the representation of cooperative social behavior (Leube et al., 2012). Alterations in precuneus activation during mentalizing have been linked to schizophrenia in several studies, some studies reporting hypo-, others hyperactivation (Bosia et al., 2012). The performance in episodic memory retrieval (i.e., recollecting events from the past) significantly explained variance in mentalizing skills (in story-based tasks) of individuals with schizophrenia (Corcoran & Frith, 2003), and memory-related processes were relevant in creating a representation of others' minds in comparable gambling tasks (Bitsch, Berger, Nagels, Falkenberg, & Straube, 2018b). A higher activation of precuneus was also observed in tasks of self- compared to other-processing (Kircher et al., 2000). Disturbances of self-processing are considered as a core feature of schizophrenia. For instance, self-face recognition was found to be impaired in schizophrenia patients (Kircher, Seiferth, Plewnia, Baar, & Schwabe, 2007), and to be altered in persons with elevated schizotypy (Platek & Gallup, 2002). Brent et al. (Brent, Seidman, Thermenos, Holt, & Keshavan, 2014) put forward that an aberrant function of brain regions implicated in the "neural circuitry of self" may constitute an "early, premorbid (i.e., pre-prodromal) indicator of schizophrenia risk". Higher brain activation can be interpreted as the higher recruitment of a certain brain function or as a compensatory mechanism for functional deficits, while lower brain activation might represent a lower engagement or a more efficient processing. Therefore the higher activation of precuneus in disorganized schizotypy could be related to compensatory mechanisms in mentalizing and self-processing (compare Cohen et al. (2015)) or higher mentalizing activity, while the lower precuneus activation in interpersonal schizotypy could be explained by reduced or (even though less likely) a more efficient self-processing and mentalizing.

The precuneus is densely connected to the cingulate cortex, the parietal and prefrontal cortex, the caudate nucleus and the parietooccipital area (Cavanna & Trimble, 2006). In our study mentalizing-related activation in the superior occipital gyrus was associated with interpersonal schizotypy negatively, and with disorganized schizotypy positively. The superior occipital gyrus was found to be activated during the mental rotation of objects (Kosslyn, Di Girolamo, Thompson, & Alpert, 1998) and presumably provides the individual with a relevant cue for self-other differentiation during mental spatial transformations (Jeannerod & Anquetil, 2008). The occipital gyrus has been hypo- or hyperactivated during mentalizing in patients with schizophrenia compared to controls in several studies (Bosia et al., 2012), and the right middle / superior occipital gyrus showed decreased activation in hallucination-prone adolescents during mental action simulation of the third compared to the first person perspective (Dahoun et al., 2013). We surmise that the activation in superior occipital gyrus might be linked to variations in visual imagery processes related to self-other differentiation.

Interpersonal schizotypy was also negatively associated with caudate nucleus activation. The caudate nucleus is part of the striatum containing a high density of dopaminergic receptors and is involved in reward-based learning (Haber & Knutson, 2010) and in mentalizing (Mar, 2011). Dopaminergic dysregulation is a hallmark of schizophrenia, and has also been reported among first-degree relatives of patients with schizophrenia and among ~~highly schizotypal~~ individuals with elevated schizotypy (Debbané et al., 2016). In patients with schizophrenia reduced right caudate (Brüne et al., 2008) and striatal activations (Lee, Quintana, Nori, & Green, 2011) have been observed during mentalizing, and alterations in striatal activity have been linked to attenuated prediction-error signaling in schizophrenia patients (Morris et al., 2012) and in individuals high in schizotypy (i.e., showing magical beliefs) (Corlett & Fletcher, 2012).

Hence, in sum, our data suggest that interpersonal schizotypy is associated with task-related altered striatal prediction-error signaling, and with altered activation in brain regions involved in self-processing, episodic memory retrieval, imagery and mentalizing. Interestingly, hypo- or hyperactivation of these brain regions has also been observed in patients with schizophrenia during mentalizing.

Disorganized schizotypy was positively correlated with activation in the right cerebellum and left middle cingulate cortex (in the analysis of the whole sample, but not in the comparison of the extreme schizotypy groups). The cerebellar lobules V and VI are involved in fine motor tasks such as finger tapping (Stoodley, MacMore, Makris, Sherman, & Schmahmann, 2016). In behavioral studies schizotypy was associated with deficits in fine motor tasks (Lenzenweger & Maher, 2002), and upper body movement abnormalities (Mittal et al., 2007). In unaffected siblings of schizophrenia patients, but not in healthy controls, higher total and disorganized schizotypy symptoms were related to more neurological soft signs (Mechri et al., 2010). Finger movements (of the right hand) were required in our task for the button presses. We speculate that the association between disorganized schizotypy and cerebellar activation could be indicative of neurological soft signs involving cerebello-thalamo-prefrontal abnormalities (Ettinger et al., 2015). An alternative interpretation is conceivable, too: A cerebellar region directly neighbored to the one identified in our task showed a higher activation in self- versus other-processing tasks (Kircher et al., 2000). Accordingly, our data could suggest that disorganized schizotypy is related to the higher recruitment of a cerebellar brain area involved in self-processing.

The middle cingulate cortex is implicated in cognitive control, decision making, mentalizing and body orientation, and partly contains high levels of dopamine and dopamine receptors (Abu-Akel & Shamay-Tsoory, 2011; Shackman et al., 2011; Vogt, 2016). One neuroimaging study showed that self-reflection in patients with schizophrenia compared to controls is associated with elevated activation of bilateral middle and posterior cingulate cortices, and lower functional connectivity between left middle-/posterior cingulate cortex and left anterior cingulate cortex (Holt et al., 2011).

In sum, our data therefore provide evidence that disorganized schizotypy is related to altered activation in brain areas that are also affected in schizophrenia and that are implicated in self-reflection, imagery, decision making, self-processing, episodic memory retrieval, fine motor functions and mentalizing.

We could not replicate the association between frontal mentalizing-related neural correlates and the cognitive-perceptual schizotypy dimension (Modinos et al., 2010; van der Meer et al., 2013). Possibly, the lack of association with frontal activation during mentalizing could be explained by the reduced demand on executive functions in our task compared to story-based, explicit mentalizing tasks. However, the scores of the cognitive-perceptual schizotypy dimension and their reliablity were rather low in our sample. Therefore the interpretation of our results for the cognitive-perceptual schizotypy dimension should be considered as tentative. Interpersonal and disorganized schizotypy were not significantly associated with mentalizing-related neural activation in frontal areas either (but see also 4.3.), however, they interacted significantly on mentalizing-related neural activity in right superior and middle frontal gyri: Subjects with higher scores in both dimensions showed a lower neural activity in these areas, while subjects with higher scores in one, but not the other dimension activated these frontal regions to a higher extent. Interestingly, a higher activation in the right middle and superior frontal gyri (among others) has also been shown in individuals with high versus low positive schizotypy during a Cartoon task (Modinos et al., 2010). The higher activation was interpreted either as greater effort compensating for an impaired mentalizing circuitry or as a tendency to over-mentalize. Similarly we would argue that individuals with elevated scores in only one schizotypy dimension might compensate deficits in the neural mentalizing network with enhanced frontal activation, but when both schizotypy dimensions are elevated, this compensatory mechanism might break down. Alternatively, we cannot rule out that individuals with a higher score in one schizotypy dimension tend to over-mentalize, and this tendency might vanish when both schizotypy dimensions are elevated. A hypo- or hyperactivation of right middle and superior frontal gyri has also been observed in subjects with schizophrenia (Benedetti et al., 2009; Bitsch et al., 2018a; Pedersen et al., 2012) and in relatives discordant for schizophrenia (de Achával et al., 2012; Marjoram et al., 2006). In sum, interpersonal and disorganized schizotypy interacted on brain regions that were found to be affected in schizophrenia and schizotypy during mentalizing.

4.3 Schizotypy and cooperative behavior

On the behavioral level (after removal of one outlier) no significant associations between the schizotypy dimensions and cooperativity of behavior were observed. On the neural level, individuals high in interpersonal and cognitive-perceptual schizotypy, but not those high in disorganized schizotypy, activated mentalizing-related brain areas (including frontal areas such as bilateral inferior and middle frontal gyrus, parietal, temporal, occipital and cerebellar cortices for interpersonal schizotypy, and left middle / superior frontal gyri and bilateral thalami and caudate nuclei for cognitive-perceptual schizotypy) to a higher extent after mutual defection compared to unreciprocated defection. We speculate that individuals higher in interpersonal and cognitive-perceptual schizotypy respond to mutual defection with a higher recruitment of mentalizing processes. As each game outcome was also related to a different combination of wins and losses, the neural activation patterns could as well be ascribed to the variation in reward. Reward processing in decision making is considered to be primarily associated with orbitofrontal-striatal circuit activation (including the caudate nucleus) (Montague & Berns, 2002). In addition, reciprocated versus unreciprocated cooperation in the PDG game was shown to be associated with higher activation of the ventral caudate nucleus and the medial frontal gyrus which was interpreted as reward-dependent learning by prediction errors (Rilling et al., 2004a). Hence we suggest that cognitive-perceptual schizotypy was also positively related to reward processing in the caudate nucleus after mutual compared to unreciprocated defection.

Conversely, reciprocated compared to unreciprocated cooperation was accompanied by higher activation of left anterior (BA 33) and middle cingulate cortex and insula in individuals with higher interpersonal schizotypy. The insula likely plays a core role in subjective feeling states attaching incentive values to behavior and salience to events (Namkung, Kim, & Sawa, 2017), and the BA33 is part of the affective division of the ACC connected to limbic areas including the insula (Bush, Luu, & Posner, 2000). The left forebrain might be related to parasympathetic activity, safety, positive affect, and social approach as proposed by Craig (2005) (but findings are partly conflicting with this proposal) (Craig, 2005). We assume that reciprocated cooperation elicits stronger positive affective responses in subjects higher in interpersonal schizotypy. This is especially interesting as interpersonal schizotypy is characterized by social anhedonia. Reciprocated cooperativity can be viewed as an unambiguously positive interaction. It is also related to a higher gain of game points for the participant compared to unreciprocated cooperation. However, it is unlikely that the affective response is solely related to reward processing as we did not observe activation differences in the reward circuitry. We speculate that individuals with elevated interpersonal schizotypy are responsive to and enjoy unambiguously positive interactions, but might in general interpret or experience social interactions as rather negative or rejecting which as a consequence might evoke their social withdrawal behavior.

Conversely, unreciprocated compared to reciprocated cooperation was related to higher activation in left precuneus and middle frontal gyrus when both interpersonal and disorganized schizotypy were elevated. We assume that this could be interpreted as an enhanced recruitment of mentalizing processes during unreciprocated compared to reciprocated cooperation.

In sum, our study revealed distinct mentalizing-related activation patterns for elevated interpersonal and disorganized schizotypy in several brain areas. This finding lends further support for the notion of heterogeneity and multidimensionality of schizotypy and schizophrenia spectrum diorders (Cohen et al., 2015; Kwapil et al., 2013). It has been put forward that the heterogenous structure has to be taken into account for the etiology, prediction and treatment of schizophrenia spectrum disorders (Kwapil et al., 2013). Several studies showed that elevated measures of schizotypy in a general population are associated with the development of a psychotic disorder later on (Debbané et al., 2015). Hence it would be interesting to investigate whether the in our study observed alterations in brain activity are stable over time and whether they have predictive value for the development of subclinical or clinical schizophrenia spectrum symptoms.

Our PDG task involved the first-person perspective in an implicit mentalizing task and we found that brain areas involved in self processing were differently activated in individuals with elevated schizotypy. Disturbances of the pre-reflective self are considered as a prominent feature in schizophrenia spectrum disorders and in its prodromal phase (B. Nelson et al., 2009). We propose that brain activation patterns associated with schizotypy during a PDG might be a useful endophenotype for the investigation of schizophrenia risk factors.

4.4 Limitations

Interactive games are considered as a more ecologically valid model for the assessment of mentalizing processes than “offline” mentalizing tasks because they are socially interactive, provide feedback and allow for implicit mentalizing. They also demand less language and executive function processing than story-based tasks (Chan & Chen, 2011; Mar, 2011). However, they also involve other cognitive and emotional processes such as perception, memory, decision making, reward processing, motivation for cooperation or competition, etc. (see e.g., Bitsch et al., 2018b). Partly, we would argue, it is inevitable that a mentalizing task includes other cognitive and emotional processes because mentalizing is a metacognitive process (i.e., monitoring of mental states of self and others) (Frith, 2012). But as a consequence, likely not all observed brain activation is linked to the mentalizing process itself. Our control condition comprised visual, motor and decision making aspects of the task, but it did not include reinforcement or changes in reinforcement. Therefore we can not rule out that task-related activity is also associated with reward processing in addition to mentalizing-associated processes. Reward processing in decision making is primarily associated with orbitofrontal-striatal circuit activation (Montague & Berns, 2002). Striatal activations in our task might therefore be ascribed to reward processing as well.

In order to reduce potential confounder effects we attempted to investigate a rather homogenous sample by including only students in our study. However the generalizability of the study results may thereby be limited.

In our sample the scores of cognitive-perceptual schizotypy were rather low compared to other studies (e.g., Fonseca-Pedrero et al., 2018). This could account for our failure to find associations of cognitive-perceptual schizotypy with mentalizing-related neural activity in frontal brain areas.

4.5 Conclusion

Our study in a large group of healthy subjects showed that the interpersonal and disorganized schizotypy dimensions display distinct associations with neural correlates of mentalizing in brain regions that have been linked to mentalizing in schizophrenia. The identified brain areas are involved in self-processing, imagery, episodic memory retrieval, and mentalizing. Interpersonal schizotypy was additionally related to striatal prediction-error signaling and disorganized schizotypy to fine motor coordination and self-reflection. Further, interpersonal and disorganized schizotypy interacted on mentalizing-related neural activation in the right prefrontal cortex.

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Conflicts of interest

None declared

Table 1: Descriptive information for the schizotypy measures (N=164)

The mean values, standard deviations (SD), ranges and the Pearson Product Moment correlation coefficients of the SPQ-B scores and age as well as descriptive information for sex (including partial eta-squared effect sizes (η^2) for significant results) are listed.

Variable	**Mean ± SD (observed range)**	**Sum ± SD (observed range)**	**Pearson Product Moment correlation coefficient**					**ANOVA F-value**
			TOTAL	**CP**	**INT**	**DIS**	**Age**	**Sex**
SPQ-B total (TOTAL)	0.16± 0.13 (0.00-0.50)	3.62± 2.75 (0-11)	-	0.35**	0.71**	0.59**	-0.01	2.38
SPQ-B cognitive-perceptual (CP)	0.09± 0.11 (0.00-0.50)	0.68± 0.90 (0-4)		-	0.10	0.06	0.03	0.68
SPQ-B interpersonal (INT)	0.23± 0.23 (0.00-0.88)	1.87± 1.83 (0-7)			-	0.28**	<0.01	0.47
SPQ-B disorganized (DIS)	0.18± 0.21 (0.00-0.83)	1.06± 1.28 (0-5)				-	-0.04	8.81** (η^2=0.05)
Age	23.97± 3.09 (19-35)						-	3.68
Sex (m/f)	86/78							-

*p<0.05, ** p<0.01

Table 2: Descriptive information for the playing behavior and its association with schizotypy measures (N=164)

The mean values, standard deviations (SD), ranges and the Pearson Product Moment correlation coefficients of the SPQ-B scores, age and playing behavior are given (the coefficients of the partial correlation controlling for age and sex are given in brackets). In the last column the F-values for sex differences are listed. CP= cognitive-perceptual, INT= interpersonal, DIS= disorganized, η^2 = partial eta-squared effect size.

Variable	**Mean ± SD (observed range)**	**Pearson Product Moment correlation coefficient**					**ANOVA F-value**
		TOTAL	**CP**	**INT**	**DIS**	**Age**	**Sex**
C (N=164)	38.28±15.87 (8-74)	0.08 (0.05)	0.01 (0.02)	0.08 (0.06)	0.05 (0.01)	0.13	5.5* (η^2=0.03)
C/D after CC	1.04±1.14 (0.00-5.75)	0.13 (0.11)	<0.01 (0.01)	0.11 (0.10)	0.13 (0.10)	0.09	3.4
C/D after CD	0.50±0.51 (0.00-2.25)	-0.01 (-0.04)	-0.03 (-0.02)	0.04 (0.03)	-0.06 (-0.11)	0.03	6.5* (η^2=0.04)
C/D after DC	0.82±1.01 (0.00-10.00)	-0.06 (-0.06)	-0.07 (-0.07)	-0.10 (-0.10)	0.06 (0.06)	0.05	0.2
C/D after DD	0.42±0.42 (0.00-4.00)	0.17* (0.18*)	0.03 (0.02)	0.17* (0.17*)	0.09 (0.13)	0.20*	1.1

*p<0.05, ** p<0.01

Table 3: Association between schizotypy scores and mentalizing-associated neural activations (whole-brain analyses, n=164)

One-sample t-tests were computed. No significant results were found for the correlations with the total score and the cognitive-perceptual dimension of SPQ-B, for positive correlations with the interpersonal dimension and negative correlations with the disorganized dimension of SPQ-B.

Anatomical region	Brain Area		x	y	z	t	k	P(FWE, peak)
SPQ-B interpersonal – negative correlation								
Precuneus, cuneus, calcarine gyrus, cerebellar vermis	Lobule V/VI	L/R	-10	-60	20	4.26	215	0.165
Olfactory cortex, caudate nucleus (extending into anterior cingulate cortex)	BA 33/s24/25	L/R	6	20	-4	3.88	61	0.453
Precuneus, calcarine gyrus, cuneus, lingual gyrus	HOc1/2	R	16	-58	18	3.77	215	0.568
Superior occipital gyrus, cuneus	hOc4d	R	20	-86	32	3.50	65	0.836
SPQ-B disorganized – positive correlation								
Precuneus, cuneus, superior occipital gyrus		R	18	-60	38	4.77	205	0.029
Superior and middle occipital gyrus	HOc4d, PGp	L	-24	-88	36	4.44	176	0.092
Cerebellar hemisphere	Lobule V/VI	R	30	-52	-26	4.00	87	0.342
Middle cingulate cortex, superior parietal lobule	5Ci	L	-14	-40	32	3.96	83	0.377
Cerebellar hemisphere and vermis, lingual gyrus	Lobule V/VI, hOc2/3v	R	10	-54	-10	3.91	257	0.423

Table 4: Association between schizotypy and mentalizing-related neural activations – comparison of game scores

The association between schizotypy dimensions and mentalizing-related neural activity of selected game scores was compared: (CC>CD), (CC<CD), (DC>DD), (DC<DD). No significant results for the contrasts (CC < CD), (DC > DD) and (CC > CD) of the cognitive-perceptual dimension, for the contrasts (CC < CD) and (DC > DD) of the interpersonal dimension, and for all investigated contrasts of the disorganized dimension were observed.

Anatomical region	**Brain Area**		**x**	**y**	**z**	**t**	**k**	**P(FWE, peak)**
SPQ-B cognitive-perceptual								
DC < DD								
Middle and superior frontal gyri	Fp1	L	-24	44	4	4.32	179	0.116
Thalamus (temporal and prefrontal), caudate nucleus	Thal	L/R	6	-6	14	3.98	149	0.338
Thalamus (prefrontal) caudate nucleus, putamen, pallidum	Thal	R	14	-2	2	3.46	53	0.876
SPQ-B interpersonal								
CC > CD								
Middle and anterior cingulate cortex	BA 33	L	-12	6	30	4.39	77	0.087
Unspecified		R	20	-12	36	4.19	178	0.175
Insula, rolandic operculum		L	-40	2	12	3.94	57	0.370
DC < DD								
Inferior frontal gyrus (pars triangularis and opercularis), post- and precentral gyrus	BA45/44, OP4	L	-52	22	16	4.15	315	0.199
Posterior and middle cingulate cortex		L/R	8	-36	30	4.11	352	0.230
Precuneus, cuneus, middle and superior occipital gyrus, calcarine gyrus, superior and inferior parietal lobule	HOc3d/2, 7M (SPL), hIP3 (IPS)	L/R	10	-64	24	4.07	752	0.261
Superior occipital gyrus, cuneus, precuneus		R	22	-64	34	3.96	164	0.352
Cerebellar hemisphere and vermis	Lobule I-IV/ V	L	-6	-38	-12	3.83	123	0.486

Calcarine gyrus	hOc1/2	R	24	-66	12	3.83	48	0.491
Middle temporal gyrus	PGa (IPL)	R	50	-50	6	3.79	165	0.536
Middle frontal gyrus	Fp1	R	36	52	6	3.78	96	0.542
Cerebellar hemisphere (including crus II)	Lobule VIIa/b	R	26	-68	-50	3.78	73	0.549
Middle and inferior frontal gyrus (pars opercularis)		R	44	22	36	3.77	62	0.562
Middle frontal gyrus, middle orbitofrontal gyrus	Fp1	L	-34	50	14	3.75	285	0.583
Middle frontal gyrus, inferior frontal gyrus (pars opercularis and triangularis)	BA45	R	46	32	22	3.68	119	0.664
Cerebellar vermis and hemisphere	Lobule V/VI	R	10	-58	-12	3.44	53	0.890

Figure 1: Association of schizotypy with mentalizing-related neural correlates

Whole-brain maps are depicted on the left showing significant clusters of a) the positive association between mentalizing-related neural activity and disorganized schizotypy (red) and b) the negative association between mentalizing-related neural activity and interpersonal schizotypy (blue). For illustrative purposes the association between all three schizotypy dimensions and the cluster eigenvariates of the right precuneus (x/y/z= 18/-60/38) [contrast: positive correlation between disorganized schizotypy and mentalizing-related neural activity (ment > con)] is shown on the right (Pearson Product Moment correlation coefficients: r(cognitive-perceptual)= 0.03, r(interpersonal)= - 0.07, r(disorganized)=0.34).

Association of schizotypy with mentalizing-related neural correlates

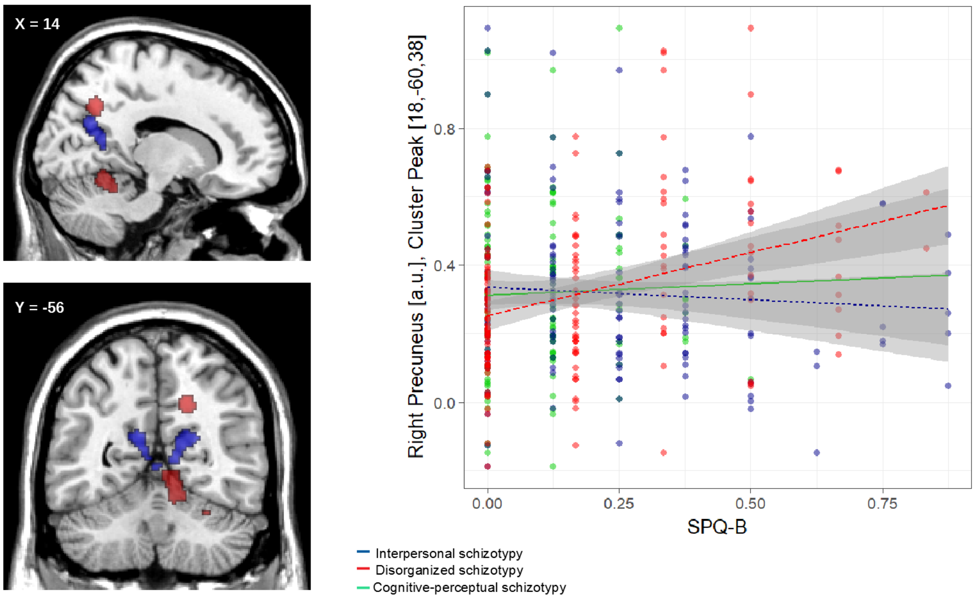
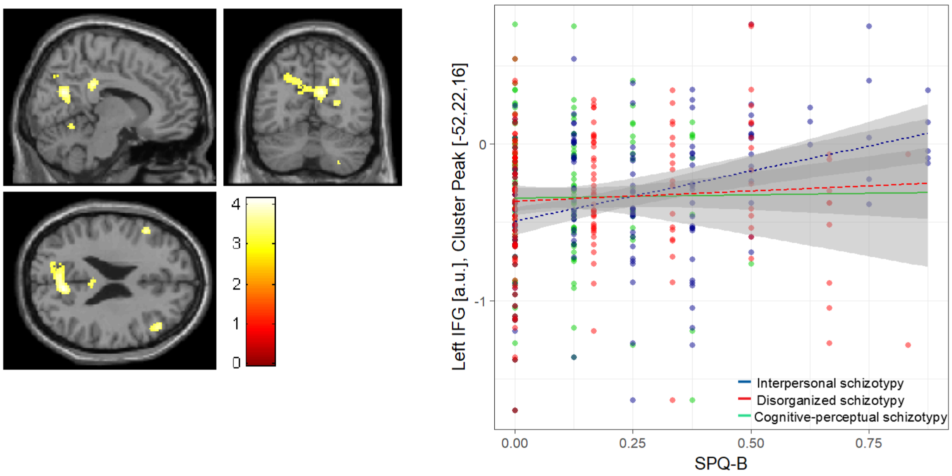


Figure 2: Association of mentalizing-related neural activation with interpersonal schizotypy after mutual defection compared to unreciprocated defection [contrast:(DC<DD)]

Whole-brain activation maps of the contrast (DC<DD) for interpersonal schizotypy are shown on the left. For illustrative purposes the association between the cluster eigenvariates of left inferior frontal gyrus (IFG) (x/y/z= -52/22/16) and all three schizotypy dimensions are depicted on the right (Pearson Product Moment correlation coefficients: r(cognitive-perceptual)= 0.01, r(interpersonal)= 0.34, r(disorganized)=0.07).

Interpersonal schizotypy and mentalizing-related neural correlates for (DC<DD)



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