Brain correlates of recognition of communicative interactions from biological motion in schizophrenia

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Background. Recognition of communicative interactions is a complex social cognitive ability which is associated with a specific neural activity in healthy individuals. However, neural correlates of communicative interaction processing from whole-body motion have not been known in patients with schizophrenia (SCZ). Therefore, the current study aims to examine the neural activity associated with recognition of communicative interactions in SCZ by using displays of the dyadic interactions downgraded to minimalistic point-light presentations.

Methods. Twenty-six healthy controls (HC) and 25 SCZ were asked to judge whether two agents presented only by point-light displays were communicating or acting independently. Task-related activity and functional connectivity of brain structures were examined with General Linear Model and Generalized Psychophysiological Interaction approach, respectively.

Results. HC were significantly more efficient in recognizing each type of action than SCZ. At the neural level, the activity of the right posterior superior temporal sulcus (pSTS) was observed to be higher in HC compared with SCZ for communicative *v.* individual action processing. Importantly, increased connectivity of the right pSTS with structures associated with mentalizing (left pSTS) and mirroring networks (left frontal areas) was observed in HC, but not in SCZ, during the presentation of social interactions.

Conclusion. Under-recruitment of the right pSTS, a structure known to have a pivotal role in social processing, may also be of importance for higher-order social cognitive deficits in SCZ. Furthermore, decreased task-related connectivity of the right pSTS may result in reduced use of additional sources of information (for instance motor resonance signals) during social cognitive processing in schizophrenia.

Introduction

Recognition and appropriate interpretation of communicative intentions is one of the essential abilities that enable one to navigate social interactions. In healthy individuals, both recognition of another person's communicative intentions (Ciaramidaro *et al.* 2014) and observation of dyadic interactions of other agents (Georgescu *et al.* 2014; Eskenazi *et al.* 2015; Quadflieg *et al.* 2015) were found to elicit increased activity in specific networks of brain structures. These structures constitute mentalizing network (bilateral posterior superior temporal sulcus (pSTS), temporo-parietal junction (TPJ) and medial prefrontal cortex (mPFC)) and action observation (mirroring) network (bilateral inferior frontal gyrus (IFG), premotor cortex (PMC), supplementary motor area (SMA), intraparietal sulcus (IaPS)) (Centelles *et al.* 2011).

Furthermore, it was proposed that even in the absence of other cues, information that is conveyed by the motion of the whole body is sufficient for healthy individuals to effectively detect communicative interactions (Manera *et al.* 2015). Point-light motion displays (PLD), a methodology introduced in the 1970s by the Swedish psychologist Johansson (1973), is the most common way to examine the processing of social information while limiting and precisely controlling the amount of visual input. Additionally, use of point-light displays allows one to examine the perception of social interactions while reducing the impact of other social perceptive abilities (for example eye-gaze processing, facial emotion recognition) or other possible confounds which may be linked to sympathy toward the agents or culturally-specific factors (Pica *et al.* 2011). Healthy individuals are able to easily differentiate situations in which two agents, who are displayed only by the point-lights attached to main joints of their bodies, are interacting with the ones where agents are acting independently (Manera *et al.* 2015). Moreover, studies investigating the 'social predictive brain' hypothesis revealed that actions

of an agent are detected more effectively under conditions of visual noise masking if they are semantically related to the actions of the other person (Manera *et al.* 2011). Also, presentation of communicative interactions between PLDs receives priority in conscious perception over the independent actions of two agents (Su *et al.* 2016). In line with these behavioral findings, recognition of social interactions *v.* individual actions is linked with neural activity in both action observation and mentalizing networks in healthy individuals (Centelles *et al.* 2011).

Schizophrenia is a severe mental disorder, which usually starts in early adulthood and profoundly impacts patients' functioning. Social cognitive deficits are considered as one of the key areas of impairment in the functioning of patients with schizophrenia. Moderate to large deficits are found in most social cognitive domains in patients with schizophrenia (Savla *et al.* 2012), and patients have been repeatedly found to present deficits in lower-level social perceptive abilities which must be drawn upon to successfully interpret complex social interactions (see Kohler *et al.* (2009) and Hoekert *et al.* (2007) for meta-analyses of studies on facial affect and verbal prosody processing, respectively, in people with schizophrenia). Thus, previous behavioral findings, suggesting reduced ability to comprehend social cues conveyed by the means of non-verbally (White *et al.* 2016) or interpret the actions and intentions of participants of naturalistic social situations (Montag *et al.* 2011; Scherzer *et al.* 2012; Rocca *et al.* 2016) in patients with schizophrenia, may stem from numerous factors associated with both lower- and higher-level processing of social information. Similarly, abnormal activity of mentalizing network, which was found in patients during processing of cooperative *v.* individual actions of two agents (Backasch *et al.* 2013) or social *v.* non-social intentions (Walter *et al.* 2009), may be linked to both lower- and higher-level social cognitive deficits which diminish patients' ability to interpret communicative interactions between real-life actors. In addition, we have previously demonstrated that patients demonstrate reduced ability to interpret the dyadic actions of two agents, even when the complexity of the stimuli has been limited by using the point-light displays of two agents (Okruszek *et al.* 2015). However, to the best of our knowledge, no previous neuroimaging study has examined processes associated with recognition of social interactions from point-light motion in schizophrenia.

Therefore, the current study seeks out behavioral and neural correlates of inferring communicative interactions in patients with schizophrenia by presenting actions of agents that have been visually degraded to PLDs. We hypothesize that in healthy controls (HC) recognition of communicative interactions from point-light motion will be linked to activation in mentalizing and action observation networks, indicating the engagement of both reflective and, more automatic, reflexive social cognitive processes during communicative interactions inference (Centelles *et al.* 2011). A recent comprehensive review of the mechanisms of social cognitive dysfunction in schizophrenia has proposed that while there is a considerable evidence for impairment of reflective social cognitive processes (e.g. mentalizing), reflexive processes (e.g. motor resonance) may be possibly intact in patients with schizophrenia (Green *et al.* 2015). In line with this suggestion and previous findings in this area, we predict that activity of mentalizing network during the processing of communicative interactions will differentiate patients from controls (Walter *et al.* 2009; Backasch *et al.* 2013). However, no discrepancies will be observed between the groups in terms of action observation network activity (Horan *et al.* 2014a). Additionally,

we aim to explore the task-related functional connectivity of structures that will be differentially activated by the processing of communicative interactions in both groups.

Methods

Participants

Twenty-five right-handed patients (age: 35.7 ± 6.9 yrs; sex: 13M/12F) diagnosed with schizophrenia according to the ICD-10 (WHO, 1992) criteria, who did not participate in our previous study (Okruszek *et al.* 2015), were recruited through leaflets in outpatient clinics in the Warsaw area. Only patients with an established diagnosis of schizophrenia, verified by the available documentation and confirmed by the clinical interview done by the qualified psychiatrist (MJ), were included in the study. Exclusion criteria included any change of pharmacotherapy during the 2 weeks prior to the study, history of comorbid head trauma, drug abuse, intellectual disability. Additionally, each patient has undergone a clinical assessment with Positive and Negative Syndrome Scale (PANSS) (Kay *et al.* 1987) and the Social and Occupational Functioning Assessment Scale (SOFAS) (Morosini *et al.* 2000) upon arrival at the testing facility. All but one medication-free patient were treated with atypical neuroleptics at the time of the study.

Twenty-six right-handed HC (age: 35.3 ± 7.1 yrs; sex: 14M/12F) with no history of psychiatric or neurological treatment or relatives diagnosed with schizophrenia were recruited through online advertisements from the same community sample.

All of the subjects (HC and SCZ) had a normal or corrected-to-normal vision and gave written consent prior to participating in the study. The procedure of the study was approved by the University of Warsaw Ethics Committee. Each participant was reimbursed (50 PLN) for participation in the study. Information on demographic and clinical variables for the participants is shown in Table 1.

Experimental task

Stimuli

The stimuli and the task for the current study have been adapted from Centelles *et al.* (2011). For the details of the stimuli production please refer to the original study. Stimuli consisted of 112 animations depicting actions of dyads of agents presented as point-light walkers (PLW). Each PLW consisted of 20 white point-lights, which had been attached to head, limbs and major joints of the body. Actions of the agents were presented against the black background. Each animation lasted 3 s. Half of the stimuli used for the current study (*n* = 56) presented social interactions (communicative actions; COM) between agents. COM animations included the conventional use of communicative gestures (e.g. agent asks other agent to sit down, another agent sits down; *n* = 23), emotional situations (e.g. agents start to jump for joy; *n* = 20) or synchronous activity of the agents during the games/dancing (*n* = 13). Actions were presented either from the forward or the sideways point of view. Furthermore, during the COM condition half of the animations was presented with an actor on the left initiating the interaction, while the other half of the animations was presented with an actor on the right initiating the interaction. During the individual condition (IND; *n* = 56) actors performed physical movements (e.g. jumps, squats down) without impacting one another.

Table 1. Characteristics of the samples

|	SCZ (n = 23)	Range	HC (n = 26)	Range	t/X^2 value
Age mean (s.d.)	35.3 (7.1)	23–45	33.6 (6.1)	21– 44	0.9
Sex (M/F)	13/10	–	14/12	–	0.03
Number of hospitalizations	4.2 (4.3)	1–15	–	–	NA
Length of illness (yrs)	10.8 (6.2)	2–24	–	–	NA
PANSS positive	11.4 (3.0)	7–19	–	–	NA
PANSS Negative	18.4 (3.8)	13–28	–	–	NA
PANSS total	57.9 (9.6)	43–80	–	–	NA
SOFAS	66.3 (13.4)	45–85	–	–	NA
CPZ equivalent (mg)	332 (213)	0–800	–	–	NA

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$; SCZ, patients with schizophrenia; HC, healthy controls; PANSS, positive and negative syndrome scale; SOFAS, social and occupational functioning assessment scale; CPZ, chlorpromazine.

Paradigm

During the experiment, both types of actions of two agents were displayed. The task was presented in two runs of 56 trials presented in an event-related design with jittered ITI of 3–5 s. After the presentation of the PLDs, the response screen with two geometric figures (green rectangle and red triangle) was shown for another 3 s. Participants were instructed to respond to the question 'Are the two persons acting together or separately?' by pressing the button of the response pad corresponding to the placement of one of the figures on the screen (green rectangle for communicative interactions, red triangle for individual actions). The order of the animations and response screens was pseudorandomized, to allow half of the animations of each type (COM, IND) to be paired with each type of the response screen. The scheme of the experimental task is shown in Fig. 1. The paradigm was created with NBS Presentation software (https://www.neurobs.com/) and displayed on a 21-inch screen which was presented to the participant with a mirror system. The scanning procedure was preceded by the training, which took place outside the scanner. During the training, a set of 24 unique animations, which have not been used during the main procedure, was presented while participants learned how to use the response pads.

fMRI data acquisitions

MRI data acquisition took place at the Laboratory of Brain Imaging, Neurobiology Center, Nencki Institute of Experimental Biology, with a 3-Tesla MR scanner (Siemens Magnetom Trio TIM, Erlangen, Germany) equipped with 32-channel phased array head coil. Functional data were acquired using a T2*-weighted gradient echo planar imaging (EPI) (parameters: TR = 2500 ms, TE = 28 ms, flip angle = 90°, matrix 64 × 64 mm, FOV = 216 mm, and 41 axial slices, slice thickness = 3 mm). There were two functional sessions (each of 234 volumes). Field mapping was done based on Jezzard & Balban's (1995) method by using double echo FLASH (TE1 = 4.92, TE2 = 7.38, time repetition = 600, same spatial parameters as functional scans). Anatomical data were acquired using a T1-weighted (T1w) sequence (parameters: TR = 2530 ms, TE = 3.32 ms, flip angle = 7°, 176 slices with an in-plane resolution of 1 mm^3, FOV = 256 mm, slice thickness = 1 mm). To ensure that group differences were not associated with motion artifacts, we inspected all the data for motion artifacts and removed the participant who showed head movements greater than 3 mm during the scanning procedure. Then, we investigated if groups differed in head motion by calculating a sum of the length of between-slices
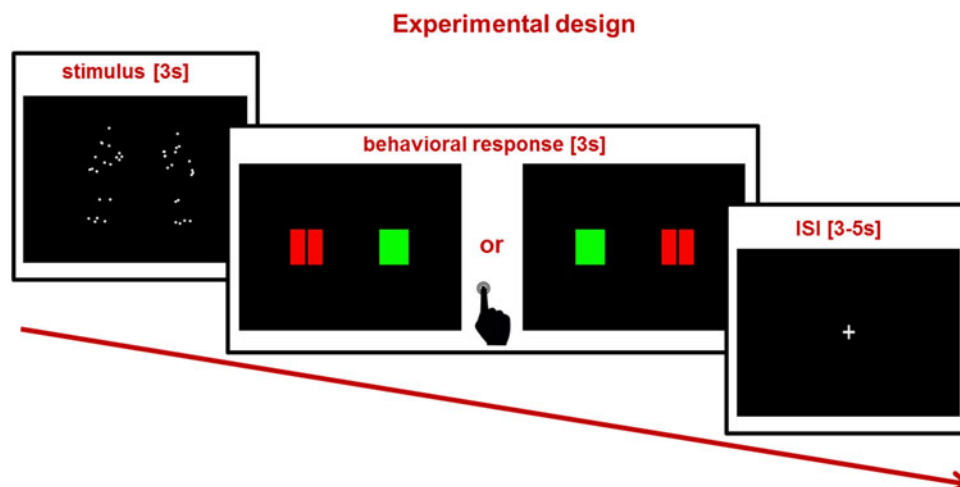
Fig. 1. Scheme of the experimental task.

translation vectors on the basis of SPM head motion regressors. No between-group differences were found for either the first ($t(47) = 1.3$ N.S.) or second ($t(47) = 1.4$ N.S.) functional block. Finally, six head motion regressors were included in the GLM first level model. Furthermore, data from one patient were discarded from further analyses, due to the lack of behavioral response to the task ($n = 1$).

Behavioral analysis

Repeated-measures ANOVA with Type (COM, IND) as a within-subject factor and Group (HC, SCZ) as a between-subject factor was used to examine the factors impacting behavioral accuracy during the task. All of the reported results were Greenhouse-Geisser corrected. The same statistical approach was adapted to analyze the reaction time data. Spearman's rho was applied to examine the relationship between overall task accuracy and RTs in patients and clinical variables (age of onset, number of hospitalizations, PANSS Positive and Negative subscales, SOFAS score). To account for the multiple comparisons, the threshold for significance was corrected to $p = 0.01$ for correlational analyses.

Neuroimaging data

General linear model (GLM) analysis

The Statistical Parametric Mapping (SPM12, Wellcome Trust Center for Neuroimaging, London, UK) toolbox was used for data preprocessing and the statistical analyses. In order to minimize geometrical distortions in EPI images caused by field inhomogeneities we used additional B0 field map scans. The FieldMap toolbox was used to calculate voxel maps displacement. Functional images were motion-corrected and unwrapped from susceptibility artifacts. Structural images (T1w) from single subjects were co-registered to the mean functional image. Then, T1w scans were classified into grey and white matter and also cerebrospinal fluid using the 'New Segmentation' tool (based on Gaussian models and also tissue probability maps). The functional images were normalized to a 2 mm isotropic voxel size and smoothed with a 5 mm isotropic Gaussian kernel.

The design for the GLM included five conditions: presentation of correctly classified COM animations, presentation of incorrectly classified COM animations, presentation of correctly classified IND animations, presentation of incorrectly classified IND animations and presentation of response (RESP) screen and six head motion regressors.

At the first-level analysis, a statistical image for the contrast between correctly classified animations containing social interactions (COM) and correctly classified animations presenting two non-interacting agents (IND) was created for each participant. At the second-level analysis, all of the COM v. IND contrast images obtained at the 1st level were included in the two-sample t test model. To minimize type I error, baseline p was set at 0.0001 and cluster size was FWE corrected ($k \geqslant 26$) to obtain $p = 0.05$.

Functional connectivity analysis

To investigate the task-related connectivity of structures that are differentially activated by the processing of communicative interactions in both groups, functional connectivity analyses were computed based on GLM findings. A mask of the right pSTS cluster which had been based on the contrast of activation of HC > schizophrenia patients for the COM v. IND contrast in a GLM

analysis was used as a seed region. The CONN functional connectivity toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012) was employed. Preprocessed data were high-pass 0.008 Hz filtered. Six motion parameters, scrubbing parameters, as well as main condition effects and five variables associated with the blood-oxygen-level-dependent (BOLD) signal from white matter and cerebrospinal fluid, were added as potential confounders for the denoising step. Generalized psychophysiological interaction (gPPI) was used to investigate the right pSTS cluster connectivity change for the COM v. IND contrast. Separate PPI maps were extracted for HC, SCZ and between-groups contrasts with a threshold $p < 0.001$ FWE corrected ($k \geqslant 48$) to obtain $p = 0.05$.

Results

Behavioral results

A main effect of Group was found ($F(1,47) = 8.2$; $p < 0.01$, $\eta_p^2 = 0.15$) with an overall lower accuracy in patients than in controls (HC: 99% ± 1% v. SCZ: 96% ± 4%). An effect of Type was also observed, with lower accuracies for the COM compared with IND condition ($F(1,47) = 5.9$, $p < 0.05$, $\eta_p^2 = 0.11$ COM: 97% ± 4% v. IND: 98% ± 3%). No interaction between Group and Type was observed ($F(1,47) = 2.9$ N.S., $\eta_p^2 = 0.06$). Patients' social functioning, as measured with SOFAS, was linked to their overall behavioral accuracy during the task ($\rho = 0.61$, $p = 0.003$); no other clinical variables were associated with the behavioral performance in patients. In an additional step of the analysis, we have calculated a correlation coefficients between clinical factors and number of errors which have been linked specifically to a/ overinterpretation of individual actions as an communicative interaction (overmentalizing) and b/ classifying the interaction as an individual actions of two agents (undermentalizing), as both types of errors have been suggested to be differentially linked to symptoms of schizophrenia (Frith, 2004). The results of the analysis revealed the correlation between the number of individual actions misclassified as communicative ones and SOFAS scores ($\rho = -0.54$, $p = 0.008$) and, surprisingly, PANSS negative symptoms ($\rho = 0.56$, $p = 0.006$).

For the RTs a main effect of Group was found ($F(1,47) = 5.9$, $p < 0.05$, $\eta_p^2 = 0.11$) with slower responses in patients than in HC($730 ± 173$ ms v. SCZ: $864 ± 214$ ms). No effect of Type ($F(1,47) < 0.1$ N.S., $\eta_p^2 = 0.001$) or interaction between Group and Type ($F(1,47) = 0.2$ N.S., $\eta_p^2 = 0.03$) were observed. In patients, RTs for COM ($\rho = -0.67$, $p < 0.001$) were negatively correlated with SOFAS; no other clinical variables were linked to RTs.

Neuroimaging results

Results for the COM v. IND contrast for patients, HC and between-group comparisons are described in Table 2 and visualized in Figs. 2 and 3.

Healthy controls

Increased engagement of numerous brain structures was found in HC for communicative interactions compared with individual action processing. A robust pattern of activity was found in the temporal cortices with clusters found in the right STS, extending from the right anterior temporal pole (TP) to the posterior STS/TPJ, and in left posterior and, to the less extent, anterior STS.

Table 2. Brain areas showing increased BOLD response during presentation of correctly classified social interactions in comparison with correctly classified individual actions of the agents

	Brain region	MNI coordinates			#BA	*T*-stat	Voxels
		x	*y*	*z*			
	Healthy controls						
R	Superior temporal sulcus	54	0	−14	22	10.77	1777
L	Superior temporal sulcus (*posterior*)	−52	−62	10	39	9.22	1422
L	Inferior frontal gyrus	−44	26	−2	47	7.90	1333
R	Inferior frontal gyrus	50	24	−4	47	7.70	1766
L	Intraparietal sulcus	−38	−44	52	7	6.70	349
L	Thalamus	−10	−18	10	−	6.65	77
L	Superior temporal sulcus (*anterior*)	−52	−10	−12	22	6.47	117
R	Fusiform gyrus	40	−52	−14	39	6.29	124
L	Middle frontal gyrus	−38	12	28	8	6.24	333
L	Middle temporal gyrus	−52	−30	0	22	5.97	33
R	Extrastriate cortex	38	−82	16	19	5.95	417
L	Intraparietal sulcus	−26	−74	28	39	5.73	217
L	Fusiform gyrus	−42	−50	−10	37	5.63	109
L	Inferior parietal lobule	−58	−40	32	40	5.50	254
L	Middle occipital gyrus	−26	−88	0	18	5.20	50
R	Lingual gyrus	22	−90	−8	18	5.16	32
R	Intraparietal sulcus	26	−52	56	7	5.03	99
R	Somatosensory cortex	56	−20	40	1	4.96	34
L	Medial Prefrontal cortex	−4	38	44	8	4.89	47
L	Premotor cortex	−30	−8	50	6	4.72	40
R	Supplementary motor cortex	2	14	64	6	4.71	29
	Patients with schizophrenia						
L	Superior temporal sulcus (*posterior*)	−58	−62	10	39	7.26	556
R	Superior temporal sulcus (*anterior*)	54	0	−14	22	7.04	205
L	Inferior frontal gyrus (*pars triangularis*)	−50	22	2	45	6.20	154
L	Inferior frontal gyrus (*pars triangularis*)	−48	26	20	44	5.52	229
L	Intraparietal sulcus	−26	−60	58	7	5.39	91
L	Premotor cortex	−44	4	52	6	5.37	26
L	Superior temporal sulcus	−50	−6	−14	22	5.01	37
R	Superior temporal sulcus (*posterior*)	56	−44	8	22	4.57	29
	Healthy controls ⩾ patients with schizophrenia						
R	Superior temporal sulcus (posterior)	48	−56	16	39	5.18	59

Results are FWE *p* = 0.05 corrected at the cluster level (k ⩾ 26). R, right hemisphere; L, left hemisphere.

Furthermore, posterior activations were observed in bilateral fusiform gyrus (FG) and bilateral middle occipital gyrus (MOG). The increased BOLD response was also found in parietal cortices: bilaterally in the IaPS and in the left supramarginal gyrus (SMG). Frontal activations were found bilaterally in the IFG and in the left mPFC. Subcortical activity was also observed in the left thalamus (THAL). Additionally, increased engagement of motor (left PMC, right SMA) and somatosensory (right somatosensory cortex; SC) areas was observed.

Patients with schizophrenia

The pattern of structures activated by communicative *v.* individual actions processing in patients with schizophrenia corresponded with the one observed in HC. However, increased BOLD response during recognition of social interactions was found in a limited set of regions, mostly restricted to the temporal and frontal cortices in patients. Processing of communicative interaction was associated with higher activity in the left pSTS
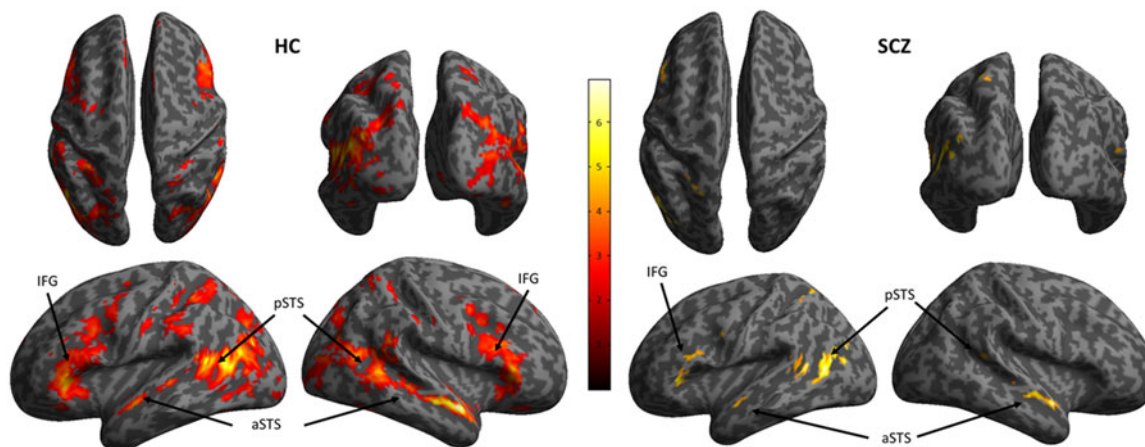
Fig. 2. Clusters of activation found at the FWE corrected *p* = 0.05 for COM *v.* IND contrasts for healthy controls (left) and patients with schizophrenia (right).

and right aSTS compared with individual actions of two agents. Two clusters of activity corresponding to the left pars triangularis were also found in the left IFG. Furthermore, increased engagement of the left IaPS and left PMC was also observed in patients during interaction recognition.

Between-group comparisons

Increased activity of the right posterior STS for the COM *v.* IND contrast was found in HC compared with SCZ. No significant clusters were found to be more activated in SCZ compared with HC. To ensure that this effect reflects the decreased activation for COM *v.* IND in patients, we extracted the mean percent signal change from the cluster identified in the GLM analysis separately for COM and IND in each group (Brett *et al.* 2002). The results of this exploratory region-of-interest analysis have revealed a significant Group by Condition interaction ($F(1,47) = 30.4$, $p < 0.001$, η_P^2 = 0.39), with increased right pSTS activity during COM, as compared with IND in HC (COM: 2.8 ± 2.0 *v.* IND: 1.9 ± 1.7, $t(25) = 6.9$, $p < 0.001$), but not in SCZ (COM: 1.4 ± 2.3 *v.* IND: 1.4 ± 2.2, $t(22) = 1.4$ N.S.). Furthermore, between-group differences with a higher signal change in HC, as compared with

SCZ were found during the COM ($t(47) = 2.3$, $p < 0.05$), but not IND ($t(47) = 1.0$ N.S.) condition.

Functional connectivity analyses

Results of the seed-based analysis are shown in Table 3. In HC increased connectivity between right pSTS and left IFG and Middle Frontal Gyrus (MFG), as well as left pSTS, was found for the COM *v.* IND contrast. No clusters of increased connectivity were found in SCZ.

Increased connectivity between the right pSTS and right cerebellar Crus II was observed in HC compared with SCZ. No clusters were found for the opposite contrast (SCZ *v.* HC).

Discussion

The aim of this study was to examine behavioral and neural correlates of processing of the communicative interactions presented only with a point-light motion in patients with schizophrenia compared with HC. The behavioral results of the study revealed that, albeit both groups were highly effective in discriminating communicative actions from individual ones, HC outperformed
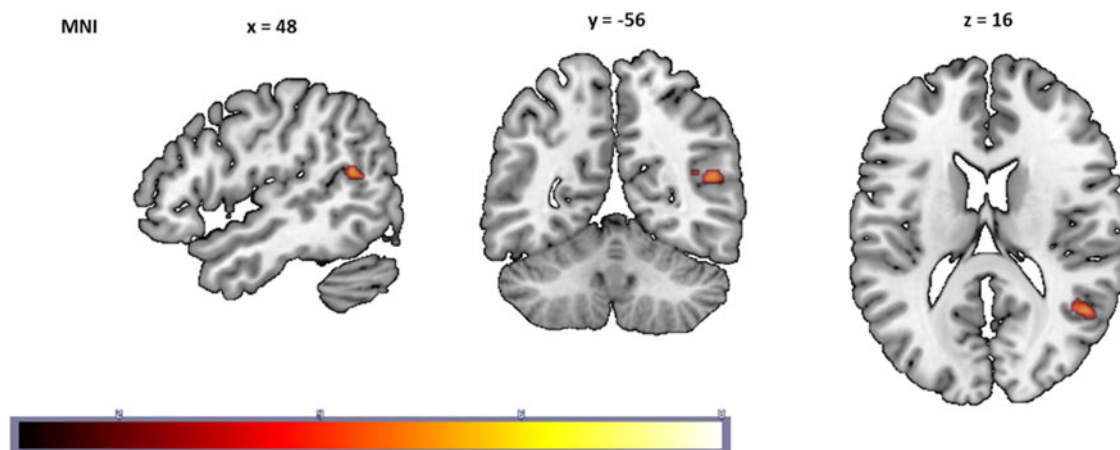

Fig. 3. A Cluster of activation which has shown higher activity for COM *v.* IND contrasts in healthy controls compared with patients with schizophrenia at the FWE corrected *p* = 0.05.

Table 3. Seed-based connection table for right pSTS for the presentation of social interactions in comparison with individual actions of the agents FWE corrected at the cluster level to $p = 0.05$ ($k \geqslant 48$)

		MNI coordinates					
	Brain region	X	y	z	#BA	T-stat	Voxels
	Healthy controls						
L	Posterior superior temporal sulcus	−58	−52	10	39	5.65	106
L	Inferior frontal gyrus/frontal orbital cortex	−40	34	−6	47	5.27	69
L	Middle frontal gyrus	−42	16	32	8	4.55	48
L	Interior frontal gyrus (*pars triangularis*)	−50	34	14	45	4.33	49
	Healthy controls ⩾ patients with schizophrenia						
R	Cerebellum (Crus II)	32	−74	−42	–	5.26	50

R, right hemisphere; L, left hemisphere.

patients with schizophrenia. Furthermore, reduced activity and connectivity of the right posterior STS was observed in patients with schizophrenia compared with controls for communicative v. individual actions processing.

Behavioral results of this study are in line with previous reports of reduced capacity to extract affective (Kern *et al.* 2013; Vaskinn *et al.* 2016) and social (Okruszek *et al.* 2015) information from point-light motion in schizophrenia. Two well-powered studies have revealed that irrespective of the type of presented emotion, medium to large deficits can be seen in patients for the recognition of affective states conveyed by PLDs (Kern *et al.* 2013; Vaskinn *et al.* 2016). The ability to infer communicative interactions from point-light motion in patients with schizophrenia was also examined in our previous study (Okruszek *et al.* 2015). Results of both studies are convergent in showing that patients display reduced accuracy in recognition of communicative interactions from point-light motion. Moreover, patients' real-life social functioning was linked to accuracy during the task. In line with previous reports of associations between 'Emotion in Biological Motion' task performance and functional capacity in patients with schizophrenia (Olbert *et al.* 2013), we argue that the link between the ability to extract social information from whole-body motion and real-life functioning of patients with schizophrenia should be further investigated.

In line with a previous neuroimaging study that used the same paradigm (Centelles *et al.* 2011), recognition of communicative interactions engaged a broad network of structures, which are critical nodes of the mentalizing network (bilateral STS and TPJ, mPFC) and action observation network (bilateral IFG, bilateral IaPS, left PMC, right SMA and SC) in healthy individuals. In patients, activations were found in structures linked with both mentalizing (left pSTS/TPJ, right anterior STS) and action observation (left IFG, left PM, left IaPS) networks. However, the pattern of activations elicited by observing the communicative interactions in comparison with the individual actions of two PLW agents in individuals with schizophrenia was not as robust as in HC. Patients' recognition of the communicative interactions elicited activity only in anterior temporal and temporo-parietal nodes of the mentalizing network, while in HC involvement of mPFC was also found. Importantly, reduced activity of mPFC during various social cognitive tasks was one of the main findings of Sugranyes *et al.*'s (2011) meta-analysis of neuroimaging studies on social cognition in schizophrenia.

However, the main finding of this study is an under-recruitment of the right pSTS during communicative interactions recognition in a group of patients with schizophrenia. Hypoactivation of certain brain regions have been repeatedly observed in patients with schizophrenia during cognitive and affective processing (e.g. ACC: Adams & David (2007); amygdala network: Li *et al.* (2010); frontoparietal network: Minzenberg *et al.* (2009)). The pSTS is believed to play a pivotal role in the perception of the dynamic aspects of human faces (Haxby & Gobbini, 2011), or the biological motion in general (Grosbras *et al.* 2012). While reduced pSTS sensitivity to the biological motion has been previously reported in patients with schizophrenia (Kim *et al.* 2011), we argue that the results of this study cannot be fully accounted for by the decreased recognition of biological motion in schizophrenia. Increased pSTS activity during communicative interactions processing was previously attributed to the detection of contingencies between the agents, rather than to processing of biological motion *per se* (Centelles *et al.* 2011). Furthermore, vignettes presenting communicative or individual actions, which have been used in this study, were identical in terms of complexity of presented biological motion, thus between-group differences in right pSTS activity cannot be explained by the processes associated with biological motion recognition.

A large body of research on the role of the pSTS in social cognitive processes provides a rationale for an alternative interpretation of the differences in the pSTS activity observed between the groups. The right pSTS is the only structure that has been repeatedly found within various methodological approaches applied by Schurz *et al.* (2014) to examine the core brain network for mentalizing in a meta-analytic review of 73 fMRI studies with healthy individuals. Furthermore, the right pSTS was found to be a region that supports a number of processes that are required to appropriately process complex social situations, namely detection of animacy (Schultz *et al.* 2005) and intentionality of actions (Saxe *et al.* 2004) as well as the integration of multimodal information about social stimuli (Kreifelts *et al.* 2009). Yang *et al.* (2015) recently reviewed the available data regarding the involvement of pSTS in social perception, action observation, and theory of mind (ToM) processes and proposed an integrative model of the role of pSTS for social cognition. The authors emphasized that due to its extensive functional connectivity, the pSTS may be treated as an intersection of three networks and that ToM

computations may be performed only after lower-level social information from social perception and action observation networks is successfully integrated in the pSTS (Yang *et al.* 2015). Finally, a recent review of the neural processes engaged in the processing of the third-party encounters (TPEs), concluded that 'the prominent role of the pSTS during the observation of TPEs does not come as a surprise. The region (…) not only implements the visual analysis of conspecifics but also contributes to interpreting their actions and internal mental states' (Quadflieg & Koldewyn, 2017, p. 7). At the same time, the authors pointed out that while there is strong support for the direct contribution of the pSTS to the analysis of scenarios with multiple agents, the extent to which specific relations between the agents modulate the pSTS activity should be further investigated.

In line with previous reports suggesting pSTS involvement in higher-order social cognitive processes, differences in pSTS activity between patients with schizophrenia and HC were observed not only during the basic social perception tasks (Kim *et al.* 2011), but also during emotion recognition (Taylor *et al.* 2012) and in a wide range of studies which examined ToM abilities with comic strip tasks (Vistoli *et al.* 2011; Ciaramidaro *et al.* 2015) or social animations (Das *et al.* 2012) as well as during the perception of (Shin *et al.* 2015) or participation in (Lee *et al.* 2014) social interactions. Similarly, in a magnetoencephalographic study, an increased activation of the right pSTS during the early stages (200–600 ms) of attribution of intentions to others (compared with the processing of physical causality with human characters) was found in healthy individuals, but not in patients with schizophrenia (Vistoli *et al.* 2011). These observations provide compelling evidence that aberrant pSTS activity in this study may be linked to the ineffective processing of social information and may be one of the mechanisms which underlie higher-order social cognitive deficits in patients with schizophrenia.

Furthermore, the role of the right pSTS connectivity in all levels of social information processing was emphasized by the results of a recent study which employed graph theory methods to study brain connectivity during the processing of different types of social stimuli (biological motion, face perception, social animations) (Dasgupta *et al.* 2016). The right pSTS was observed to be the most highly connected region, regardless of task type. The authors suggested that the pSTS may be perceived as 'a hub of the social brain' (Dasgupta *et al.* 2016), thus it may be hypothesized that it may be crucial for integration of information from various brain networks (e.g. person perception network, mirroring network, mentalizing network; Quadflieg & Koldewyn, 2017) which is necessary to correctly process communicative interactions between other persons. This notion is supported by our exploratory analyses of the right pSTS's functional connectivity during communicative *v.* individual actions processing. In HC increased connectivity was observed for the right pSTS seed both within the mentalizing network (left hemispheric pSTS regions) and with structures from action observation network (left IFG). No such effects were observed in patients with schizophrenia. Furthermore, between-group contrast revealed decreased connectivity between the right pSTS and right cerebellar Crus 2 region in patients with schizophrenia. This finding may be interpreted in terms of reduced connectivity between pSTS and mentalizing networks in patients. A rationale for such interpretation stems from Buckner *et al.*'s (2011) study, which provided a complete map of the cerebellar organization in a relationship with major cerebral functional networks on the

basis of the resting-state functional connectivity data from 1000 healthy participants. Van Overwalle *et al.* (2015*a*) observed a large overlap between regions commonly activated in the cerebellum by social cognitive tasks and default and somatomotor networks from Buckner *et al.*'s (2011) parcellation. Furthermore, evidence for a domain-specific role of cerebro-cerebellar connectivity during social cognitive processes was provided by meta-analytic connectivity modelling based on the results of 133 neuroimaging studies (Van Overwalle *et al.* 2015*b*), which has found a specific coactivation patterns between cerebellar default/mentalizing regions and cerebral mentalizing network (mPFC, TPJ, pCC) and between cerebellar somatomotor regions and cerebral action observation network (pSTS, IFG, precentral/postcentral areas). To examine the significance of the decreased pSTS-cerebellar connectivity during the communicative *v.* individual actions processing in patients with schizophrenia, we analyzed the results of our PPI analysis in relation to seven major cerebellar networks described by Buckner *et al.* (2011; http://surfer.nmr.mgh.harvard.edu/fswiki/CerebellumParcellation_Buckner2011). As may be observed in the Supplementary Fig. 1, all of the clusters of decreased pSTS-cerebellar connectivity in patients group are confined within the boundaries of cerebellar default/mentalizing network. It has been suggested, that connectivity between right posterior cerebellar 'mentalizing' areas and cerebral ToM network may be crucial for matching external information with internal predictions generated in the cerebellum (Van Overwalle & Mariën, 2016). Decreased connectivity between right pSTS and cerebellar 'mentalizing' areas may thus impact the patients' ability to use internal predictions while sequencing the actions of agents during the communicative interactions. Furthermore, this result may be seen as an adjunct to previous findings, which have documented reductions in ToM task-related connectivity in patients with schizophrenia for right pSTS connections with cerebral mentalizing network nodes, including contralateral pSTS (Mier *et al.* 2016) and medial PFC (Ciaramidaro *et al.* 2015). Additionally, the increased coupling between right pSTS and action observation network was found during communicative *v.* individual action processing only in HC. This finding may suggest that even despite motor resonance information is successfully generated in patients during social interactions processing (Horan *et al.* 2014*a, b*), it is not effectively incorporated for the communicative interactions inference and mentalizing purposes. These findings add to the previous literature that suggests that the role of the pSTS in social cognitive processes in humans extends far beyond the basic social perceptive processes. Furthermore, our results add to the mounting evidence pointing to the crucial role of the right pSTS hypoactivity and hypoconnectivity for the processes of social cognition in schizophrenia. Clinical significance of the current study is further established by the relationship which has been observed between patients' social functioning and behavioral results of the task. This finding suggests that misinterpretation of third-party encounters may be directly linked to the real-life problems observed in a social domain in schizophrenia. Another clinical implication of the current study is that right pSTS may be a suitable target for noninvasive brain stimulation therapies aimed at improving social cognition in patients with schizophrenia. The possibility of improving social cognition by using transcranial electric stimulation has been investigated so far mostly with regard to the stimulation of prefrontal areas (Sellaro *et al.* 2016), and just a few studies focused on the impact of the tDCS stimulation of the right TPJ/STS areas on social cognitive processes (Santiesteban *et al.* 2012; Mai *et al.* 2016). Given the

importance of the right pSTS for multiple levels of social cognition, future studies should examine the effectiveness of such interventions in schizophrenia.

While the findings of this study are robust, some of the study's limitations should be pointed out. We examined only clinically-stable outpatients with no acute psychotic symptoms at the time of the examination (see Table 1 for patients' PANSS scores). As revealed by previous studies, pattern of social cognitive deficits may be differentially related to the various clinical profiles observed in patients with schizophrenia (Russell *et al.* 2006; Montag *et al.* 2011; Rocca *et al.* 2016). Thus, our results should be replicated in patients with more pronounced clinical symptoms. Additionally, we did not use any additional localizer task to identify individual coordinates for the pSTS anatomical location, and no basic biological motion recognition task was applied; thus, it is impossible to estimate the extent to which between-groups differences in abilities associated with biological motion processing affected the pattern of behavioral and neural results observed during social interaction recognition. Furthermore, to avoid motor preparation processes, which could confound our findings on action observation network activity, we randomized a response screen between trials, so participants could not predict which hand would be used to provide a response (Centelles *et al.* 2011). However, it cannot be ruled out that this manipulation may have affected the behavioral and neural findings, as patients with schizophrenia have well-documented problems with task switching (Reichenberg & Harvey, 2007). Additionally, one may suggest that, as the main effect of the group was observed for the behavioral performance, the under-recruitment of the pSTS may reflect patients inability to perform the task. However, our exploratory ROI analysis confirmed that the pSTS activity showed strong modulation by the condition in HC, but not in patients and between-group differences in the pSTS activity were found to be limited to the communicative condition of the task. Finally, the stimuli used in the current study combined different types of interactions (conventional communicative gestures, affective situations, scenes from games) for the COM condition. The extent to which pSTS activity is modulated by the specific types of interactions between agents is largely unexplored (Quadflieg & Koldewyn, 2017), thus future studies should examine neural response to each of the specific TPEs types.

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