Schizophrenia Research 209 (2019) 113–128

Contents lists available at ScienceDirect

Schizophrenia Research

journal homepage: www.elsevier.com/locate/schres

Dynamics of impaired humour processing in schizophrenia – An EEG effective connectivity study

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ARTICLE INFO

Article history:
Received 6 August 2018
Received in revised form 1 February 2019
Accepted 5 May 2019
Available online 16 May 2019

Keywords:
Humour
Schizophrenia
Effective connectivity
Electroencephalography
Directed transfer function

ABSTRACT

Specific language and communication abilities, such as humour comprehension, are commonly impaired in schizophrenia. The present study investigates the dynamics of the humour-related neural network underlying this deficit. Specifically, we focused on the abnormalities of information flow in schizophrenia within the fronto-temporo-parietal circuit. We estimated the direction and strength of cortical information flow in the time course of humour processing by the EEG Directed Transfer Function. The study included 40 schizophrenia outpatients and 40 healthy controls (age-sex-education matched) assessed with an EEG punchline-based humour comprehension task (written and cartoon jokes). The linear mixed models procedure was used to test group effects across three processes: 1. incongruity detection, 2. incongruity resolution and elaboration, 3. complete humour processing. Conjunction maps for both types of jokes were created to investigate fundamental between-group differences, beyond the context of modality. Clinical subjects indicated a lower level of understanding of the funny punchlines, indicated absurd punchlines as more understandable and gave higher funniness ratings to both absurd and neutral punchlines. The EEG effective connectivity results revealed that humour processing in schizophrenia engages alternative circuits, exhibiting a pronounced abnormal leftward shifted lateralization related to diminished activity of the right hemisphere in fronto-temporo-parietal regions. In conclusion, the present paper presents the dynamics of cortical propagation of information in the humour-related circuit as a neural substrate of humour impairment in schizophrenia.

1. Introduction

Humour, a complex phenomenon which plays an important role in human social life (Polimeni and Reiss, 2006a; Veatch, 1998), is commonly impaired in schizophrenia (Adamczyk et al., 2016; Bozikas et al., 2007; Corcoran et al., 1997; Marjoram et al., 2005; Polimeni and Reiss, 2006b; Polimeni et al., 2010). Previous studies on humour emphasized the fact that individuals with schizophrenia find jokes more difficult to understand and appreciate, especially when they are mental-state-jokes (e.g. necessitate using the Theory of Mind; Corcoran et al., 1997; Marjoram et al., 2005). Other investigations reported that humour deficits in schizophrenia were related to cognitive impairments (e.g. selective attention, vigilance, phonological word fluency) (Bozikas et al., 2007) or poorer social functioning and other specific cognitive deficits (e.g. semantic cognition and executive functions) (Polimeni and Reiss, 2006b; Polimeni et al., 2010). Nonetheless, despite clear behavioural evidence, the neural substrates of this phenomenon (e.g. humour processing in schizophrenia) are still poorly known.

Recent neuroimaging studies on humour in healthy controls have usually been based on the step-by-step theory of humour comprehension and elaboration (Suls, 1972; Wyer and Collins, 1992). This theory of humour elicitation conceptualizes joke processing as 1. the cognitive process of reorganisation of detected incongruous content (i.e. incongruity detection followed by its resolution) which is necessary for further 2. the emotional process of humour elaboration resulting in the feeling of amusement (Wyer and Collins, 1992). To date, two approaches were dominant in fMRI studies to test this theory. The first one attempted to distinguish the cognitive and emotional aspects of humour processing (Amir et al., 2015; Bartolo et al., 2006; Chan et al., 2012; Franklin and Adams, 2011; Goel and Dolan, 2001; Mobbs et al., 2003, 2005; Moran et al., 2004; Wild et al., 2006), while the second one explored more subtly defined sub-processes of cognitive division (i.e. incongruity detection vs resolution; Chan et al., 2013; Dai et al., 2017; Nakamura et al., 2017; Tian et al., 2017). As a result, numerous brain structures related to different aspects of humour processing have been identified. Overall, the cognitive aspect of humour processing was associated with the dorsomedial prefrontal cortex (dmPFC), inferior frontal gyrus (IFG), anterior and posterior temporal cortices (aTL,

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https://doi.org/10.1016/j.schres.2019.05.008
0920-9964/

pTL), temporoparietal junction (TPJ) and precuneus. On the other hand, the emotional component (i.e. elaboration/amusement) involved the ventromedial prefrontal cortex (vmPFC), anterior cingulate cortex (ACC), insula, amygdala, parahippocampal gyri, caudate nuclei and the cerebellum (for review see: Vrticka et al., 2013). However, distinguishing the neural substrates of 'getting a joke' from 'appreciating a joke' turned out to be both theoretically and methodologically difficult, since performing the task of subjective rating of a joke's funniness frequently activates cognitive divisions of the humour, such as dmPFC, TPJ or precuneus (Adamczyk et al., 2017, 2018; Bartolo et al., 2006; Campbell et al., 2015; Chan et al., 2013; Goel and Dolan, 2001; Marjoram et al., 2006; Samson et al., 2008, 2009; Wild et al., 2003). Conversely, the amygdala, known as the core functional substrate of emotional evaluation, might play an important role in humour comprehension (Nakamura et al., 2017). In summary, we may assume that, even though nonspecific, the humour-related neural circuit contains fronto-temporo-parietal cortical areas such as: vmPFC, ACC, dmPFC, dlPFC, IFG, aTL, pTL, TPJ, IPL and the precuneus.

As can be seen, humour processing depends on an extensive network of brain structures which exchange information at each stage of this process. Exploring its dynamic character becomes a challenge due to limited fMRI time resolution and contribution from EEG or MEG can bring deeper insight into these rapid processes (Feng et al., 2014; Ku et al., 2017; Marinkovic et al., 2011; Shibata et al., 2017; Vrticka et al., 2013). Initially, event-related technique was applied to investigate the three-stages of humour processing in healthy individuals. It was revealed that: incongruity detection can be marked by the P2 (approx. 200–250 ms) and N400 (approx. 350–500 ms) components; incongruity resolution is related to the P600 component (approx. 500–700 ms); elaboration/amusement is related to LPP (late positive potential, approx. 700–1500 ms) (Feng et al., 2014; Ku et al., 2017; Shibata et al., 2017). It can be concluded, that successful detection and resolution of humour content is completed within around 1 s, and is followed by emotional response (amusement), lasting several seconds. Despite the controversies on validity of the three-step humour theory, the above mentioned ERP studies provide some support for the proposed division into humour comprehension sub-processes. Interestingly, the exceptional research of Iakimova et al. (2005) and Schneider et al. (2015) on figurative language processing in schizophrenia revealed alterations in the amplitude of EEG event-related potentials. Indeed, when compared to healthy controls, individuals with schizophrenia revealed nonspecific alterations related to general impairments in complex language processing manifested by larger N400 amplitudes and greater hemodynamic activations in the left hemisphere during processing of figurative, literal and nonsensical sentences (Schneider et al., 2015). This seems to support our assumption that general and nonspecific deterioration of the incongruity detection process (e.g. impaired discrimination between funny, neutral and nonsensical content) may be considered a primary source of humour comprehension deficit in schizophrenia (Adamczyk et al., 2017, 2018).

Considering our previous pioneering findings on neural substrates of humour deficits in schizophrenia, the functional deterioration of the right TPJ visible during incongruity detection may be assumed a primary source of impairment, impacting further stages of processing (Adamczyk et al., 2017, 2018). Recent advances in neuroimaging methods based on network approach may provide crucial information on the information flow within the humour-related neural circuit. In the present study, we explore the neural underpinnings of humour dynamics by adopting EEG effective connectivity in order to estimate the direction and strength of cortical information flow. The Directed Transfer Function (DTF), a method based on multivariate autoregressive modelling of time series (MVAR) that uses Granger's approach to determine the causality of brain activations (Blinowska et al., 2004) was used. Specifically, we were looking for spatiotemporal abnormalities within the fronto-temporo-parietal circuit in schizophrenia during the punchline-based humour comprehension task (Adamczyk et al., 2017); contained short stories with three possible endings (punchlines): neutral (NEU), absurd (ABS) or funny (FUN). Three experimental conditions were proposed for further analysis, in order to test the theoretical three phases of humour processing (Suls, 1972; Wyer and Collins, 1992; Chan et al., 2013). They were related to: 1. incongruity detection process contained in absurd condition (incomprehensible and not-intended-to-be-funny incongruity) operationalized as ABS-NEU difference, 2. incongruity resolution and elaboration process contained in funny condition (comprehensible and intended-to-be-funny content, but without incongruity detection element) operationalized as FUN-ABS difference; 3. complete humour processing contained in funny condition, that is FUN-NEU difference, where all humour components are present. We expected that the most essential differences would be related to the incongruity detection stage and would be manifested at the behavioural (reaction times and ratings of comprehensibility and funniness) and neural level (information flow rate between ROIs) by an impaired discrimination of absurd, funny and neutral content, together with essential suppression of cortical information flow in the right temporo-parietal structures during processing of funny content in schizophrenia, as compared to healthy controls.

2. Material and methods

2.1. Participants

The study included 40 schizophrenia outpatients and 40 healthy controls (age-sex-education matched), all of whom gave informed consent to participate in the experimental procedures, i.e. interview, Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), EEG recordings and, only in the clinical group, assessment with the Positive and Negative Syndrome Scale (PANSS; van der Gaag et al., 2006; Kay et al., 1987). All participants were remunerated after data acquisition ($n = 80$; € 10). Procedures were approved by the Bioethical Committee at Jagiellonian University in Krakow, Poland and were designed in accordance with the ethical standards of the World Medical Association Declaration of Helsinki (2013). All clinical subjects were in a stable psychopathological condition for several weeks before the experiment. None of the participants had a history of head injuries, seizures, substance dependence or any serious current somatic illnesses. All were right-handed native Polish speakers. Demographic and clinical data is presented in Table 1.

2.2. Experimental procedure

The experimental design, stimuli and procedures used in this study were analogical to those described in our previous reports (Adamczyk et al., 2017, 2018). All substantial modifications for EEG experiments are provided below. The Pictorial and written tasks were analysed separately.

Behavioural analysis included the following variables:

- independent factors:
  - group (healthy controls, schizophrenia outpatients),
  - condition (type of punchline: NEU, FUN, ABS).

- dependent variables:
  - rating of comprehensibility,
  - rating of funniness,
  - reaction time for comprehensibility,
  - reaction time for funniness.

EEG analysis included:

- independent factors:

Table 1
Demographic and clinical data.

Demographic data	Healthy controls (n=40)	Schizophrenia outpatients (n=40)	Statistics
Age	Mean (± SD) 42.75 (10.17)	Mean (± SD) 42.60 (10.12)	t = 0.07; ns Z adj. = 0.07; ns
Sex	n (%)	n (%)	
Male	19 (47.5%)	20 (50%)	Chi^2 = 0.05; ns
Female	21 (52.5%)	20 (50%)	
Education (in years)	14.70 (2.70)	14.80 (2.90)	t = - 0.16; ns Z adj. = - 0.32; ns
MoCA	26.48 (2.59)	23.90 (3.22)	t = 3.94; P < 0.001 Z adj. = 3.69; P < 0.001

Schizophrenia diagnosis:	Clinical data n (%)
- paranoid (F20.0)	34 (85 %)
- undifferentiated (F20.3)	2 (5 %)
- simple (F20.6)	1 (2.5 %)
- schizoaffective disorder (F25.0)	3 (7.5 %)
Type of pharmacotherapy:	
- atypical antipsychotics	27 (67.5%)
- typical and atypical antipsychotics mixed	11 (27.5%)
- typical antipsychotics	1 (2%)
- no antipsychotics	1 (2%)
- anxiolytics	5 (12.5%)
- antidepressants	6 (15%)
- mood stabilizers	8 (20%)
Illness characteristics:	Mean (± SD)
- duration of psychosis (in years)	19.40 (10.12)
- number of relapses	9.40 (7.40)
- number of hospitalizations	7.73 (5.13)
- Chlorpromazine equivalent (mg/day)[a]	440.00 (298.81)
PANSS	
- total	57.40 (18.34)
- positive	10.68 (4.81)
- negative	15.80 (7.23)
- disorganization	8.77 (4.09)
- excitement	6.08 (2.38)
- emotional distress	8.35 (3.03)

Demographic and clinical data. n/a - not applicable; ns - non-significant group difference.
[a] The mean dose of antipsychotics calculated as chlorpromazine equivalents (Atkins et al., 1997; Gardner et al., 2010; Woods, 2003).

- o group (healthy controls, schizophrenia outpatients),
- o condition (type of punchline: NEU, FUN, ABS),
- o ROI (20 electrodes in 9 predefined regions),
- o time window (0–1 s, 1–2 s, 2–3 s, 3–4 s, 4–5 s).

- dependent variables:
  - o effective connectivity rate (DTF)

2.2.1. Stimuli

120 funny stories (written jokes) and 120 cartoons with a single balloon or caption (pictorial jokes) in the Polish language were selected from the internet; excessively vulgar, sexist, racist, religious or political content was rejected. After selection, all jokes were modified to create three types of endings: 1. funny (FUN) - original endings which are comprehensible and intended-to-be-funny; 2. neutral (NEU) - unfunny endings which are comprehensible and not-intended-to-be-funny, or 3. absurd (ABS) - nonsensical endings which are incomprehensible and not-intended-to-be-funny and were then presented to 60 healthy people for ratings of comprehensibility and funniness on a 1–9 Likert scale (from 1 = totally incomprehensible/unfunny to 9 = totally comprehensible/funny). Finally, the stimuli selected for the experimental procedures met the following criteria for the three conditions: FUN (≥6 for comprehensibility and funniness: 8.30 ± 0.29/7.92 ± 0.42, and 6.76 ± 0.54/6.10 ± 0.57 for mean ± SD for stories/cartoons, respectively), NEU (≥6 for comprehensibility and ≤3 for funniness: 6.86 ± 0.64/6.76 ± 0.66 and 2.22 ± 0.52/2.51 ± 0.60 for mean ± SD for stories/cartoons, respectively), ABS (≤3 for comprehensibility and funniness: 2.48 ± 1.09/2.84 ± 0.96 and 1.85 ± 0.50/2.02 ± 0.46 for mean ± SD for stories/cartoons, respectively). Next, each stimuli was divided into a setup and a punchline. The setups were: 1. short stories 8–50 words long (mean = 22.48 ± SD = 8.46) for written jokes and 2. drawings without any words (e.g. blank white balloon) for pictorial jokes. The punchlines were: 1. 2–12 (mean = 6.02 ± SD = 2.69) or 2. 2–17 (mean = 7.00 ± SD = 2.82) words in length, respectively.

2.2.2. Experimental task: punchline-based humour comprehension task

All procedures were presented using PsychoPy v1.82.01 software (Peirce, 2009). The two experimental tasks (i.e. written and pictorial jokes) were presented separately in two runs using a 61 cm computer screen (ViewSonic VG2401mh). Responses were collected using a standard keyboard (left/right arrows to select a rating and Enter to accept the chosen answer). Each run included a short instruction and was followed by a few examples to practise responding before the proper test. Each participant was presented 60 stories and then 60 cartoons in randomized order; each set contained 20 items with each one of three endings (FUN, NEU, ABS). Each setup was shown for 18 s in the case of stories, and 8 s for cartoons. The punchline was shown for 8 s in both runs. Then, participants were asked to provide a subjective judgment of the comprehensibility (yes/no) and funniness (1–9 on the Likert-type scale) of the stories and cartoons. Reaction times of every rating were collected with no time restrictions for responding.

2.3. Directed transfer function

An important property of biological signals is their transient oscillatory character, which allows a signal to be predicted by observing its nearest past and estimating the parameters of an autoregressive model. In this approach, each data sample $X(t)$ can be represented as a weighted sum of p previous samples with an added random component, $E(t)$, which reflects a part of signal variability which cannot be predicted. $A(t)$ represents the model's coefficient matrix.

$$X(t) = c + \sum_{i=0}^{p} A(i)X(t-i) + E(t) \quad (1)$$

Granger causality defines a signal *X2* as causal for a signal *X1* only if *X1* can be better predicted using previous values of both signals than using past values of signal *X1* alone. This approach can be extended to multivariate data, and in this case $X(t)$ becomes a vector of multiple channels' values. The Eq. (1) can be transformed into a frequency domain:

$$X(f) = A^{-1}(f)E(f) = H(f)E(f) \quad (2)$$

where $H(f)$ can be considered as a form of linear filter:

$$H(f) = \left(\sum_{m=0}^{p} A(m)\ exp(-2\pi imf\Delta t)\right)^{-1} \quad (3)$$

Finally, a non-normalized DTF function can be written that describes the flow from channel j to channel i at frequency f:

$$\gamma_{ij}^2(f) = H_{ij}(f)\mathrm{v}^2 \quad (4)$$

The detailed description of the method is beyond the scope of this paper and more details can be found elsewhere (Blinowska et al., 2004; Kamiński and Blinowska, 1991).

2.4. EEG recording and preprocessing

EEG recording was carried out using a Biosemi Active Two amplifier and 32 active electrodes placed on a standard 10–20 headcap with 256 Hz sample rate. Four additional sensors were used for recording oculomotor activity, and two more for offline linked mastoid reference. The preprocessing was performed using EEGlab toolbox (Delorme and Makeig, 2004). It included filtering (3 to 45 Hz with zero phase-shift filters), downsampling to 128 Hz, a custom procedure for removing blink contaminations (subtracting individually fitted blink curve; Wyczesany et al., 2018), and finally epoching (time windows −1 to 5 s relative to punchline onset). Segments with artefacts exceeding the 100 μV threshold on any of the electrodes were rejected. Based on the AIC the autoregression model order was set to 8. The length of available data was then successfully checked across each subject/condition to confirm the use of the 1 s window length in MVAR modelling. The following formula was applied: W ≥ 10 (pM/N), where W – required minimum window length in samples, p – model order, M – number of channels and N – total number of epochs for all trials within each valence condition (Wyczesany et al., 2014).

As the electromagnetic fields propagate almost instantaneously in brain tissue with no apparent phase differences between electrodes, the DTF method remains relatively insensitive to the problem of volume conduction (Kaminski and Blinowska, 2014). This allows for more precise location of underlying structures using the sensor-space analysis while avoiding known problems with connectivity computations over the source-space signals (Mahjoory et al., 2017). Thus, based on the EEG montage brain atlas (Koessler et al., 2009), 20 electrodes were selected that corresponded with the regions of interest (ROIs) chosen on the basis of the existing literature and our previous fMRI findings on humour-related neural circuit (Adamczyk et al., 2017, 2018). These were: vmPFC (Fp1; Fp2; BA 10: middle and superior frontal gyri); dmPFC (Fz; BA 8/32: superior frontal gyri/dorsal anterior cingulate); the dorsolateral PFC (dlPFC: AF3, F3; AF4, F4; BA 9: middle and superior frontal gyri); IFG (F7, FC5; F8, FC6; BA 44/45: pars opercularis and pars triangularis); aTL (T7, T8; BA 21/22: middle and superior temporal gyri); pTL (P7, P8; BA 37: inferior temporal gyrus); TPJ (CP5, CP6; BA 40: supramarginal gyrus); the inferior parietal lobule (IPL: P3, P4; BA 39: angular gyrus); the precuneus (Prec: Pz; BA 7/31: superior parietal gyrus/dorsal posterior cingulate).

Non-normalized DTF values for all pairs of electrodes between all predefined ROIs were then calculated in the beta band (14 Hz–25 Hz) for all six time bins of 1 s length (from −1 to 0, up to 4 to 5 s relative to punchline onset) using Multar software (Department of Biomedical Physics, University of Warsaw, Poland). The connectivity value of the first pre-punchline bin was subtracted from all the following bins to obtain baseline corrected DTF values. To control the quality of autoregressive model fitting, residual noise matrices were determined for all subjects. The distributions of the obtained DTF values were checked to identify and reject possible extremes, which were defined as falling below Q1–1.5*IQR or above Q3 + 1.5*IQR, where Q – quartile and IQR – interquartile range (Ligeza et al., 2016).

2.5. Statistical analysis

2.5.1. Behavioural data

Individual means for ratings of comprehensibility and funniness and reaction times were computed for each condition (FUN, ABS, NEU). Due to the distributions of the variables, the between-group differences were analysed with the U Mann-Whitney test.

2.5.2. EEG data

The linear mixed models statistics from the lme4 R package (Bates et al., 2015) were used to test the effects of conditions and groups on connectivity between selected ROIs. A model with group (healthy controls, schizophrenia outpatients), condition (NEU, FUN, ABS), ROI (in total 20 electrodes forming predefined regions), and time window (0–1 s, 1–2 s, 2–3 s, 3–4 s, 4–5 s) as fixed factors and subjects as a random factor was analysed separately for written and pictorial data. In the case of within-group analysis, the group reference level was fixed to the particular group (either healthy controls or schizophrenia

Table 2
Scores and reaction times for ratings of comprehensibility and funniness.

Ratings/type of punchline	Healthy controls (n = 40)		Schizophrenia outpatients (n = 40)		Between-group difference (Mann-Whitney test)			
	Scores	Reaction times	Scores	Reaction times	Scores		Reaction times	
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Z adjusted	P-value	Z adjusted	P-value
Written-jokes								
Comprehensibility[a]								
FUN	19.63 ± 0.70	2.75 ± 1.41	17.45 ± 3.68	3.97 ± 2.20	−3.65	0.001	3.24	0.001
NEU	19.15 ± 1.97	3.30 ± 1.53	18.66 ± 2.41	4.40 ± 2.55	−1.27	0.260	2.23	0.025
ABS	19.63 ± 1.17	2.91 ± 1.31	18.35 ± 2.81	4.03 ± 1.88	−4.29	0.001	3.18	0.001
Funniness[b]								
FUN	6.88 ± 1.10	2.65 ± 1.06	6.27 ± 1.71	3.55 ± 1.62	−1.57	0.116	2.64	0.008
NEU	2.55 ± 1.33	2.91 ± 1.22	3.40 ± 2.05	3.63 ± 1.62	1.84	0.066	2.24	0.025
ABS	1.60 ± 0.73	3.09 ± 1.25	2.83 ± 1.91	3.91 ± 2.28	2.90	0.004	1.81	0.070
Cartoon-jokes								
Comprehensibility[a]								
FUN	19.40 ± 1.25	3.29 ± 2.44	17.73 ± 3.42	5.02 ± 2.72	−2.96	0.007	3.85	0.001
NEU	19.20 ± 1.11	3.76 ± 2.50	18.33 ± 2.55	5.23 ± 2.52	−1.50	0.165	3.35	0.001
ABS	17.80 ± 2.40	4.77 ± 3.29	16.28 ± 3.41	6.82 ± 3.64	−2.16	0.033	2.88	0.004
Funniness[b]								
FUN	6.63 ± 1.25	3.63 ± 1.92	6.11 ± 1.73	4.76 ± 2.25	−1.25	0.211	2.44	0.014
NEU	3.13 ± 1.50	4.25 ± 2.05	3.98 ± 1.66	5.62 ± 2.97	2.24	0.024	2.46	0.013
ABS	2.09 ± 1.02	4.05 ± 2.18	3.27 ± 1.55	5.64 ± 3.65	3.33	0.001	2.37	0.017

Scores and Reaction times for ratings were presented as mean ± standard deviation (SD) for all types of punchlines. Reaction times are presented in seconds. The significance level in all statistical analyses equalled alpha = 0.05.

[a] Sum of responses indicating the stimuli was rated as comprehensible in the case of NEU and FUN punchlines, or non-comprehensible in the case of ABS punchlines, with max score = 20 (min = 0).

[b] Mean of responses on a 1–9 Likert-type scale (max score: 9 – very funny).

outpatients). For the between-group analysis, the interaction term between condition and group was considered. Data were visualized using Trand3D 1.2 software (Department of Biomedical Physics, University of Warsaw; Blinowski et al., 2014) in three pairs of directional contrasts reflecting 1) incongruity detection (ABS vs NEU), 2) incongruity resolution and elaboration (FUN vs ABS), and 3) complete

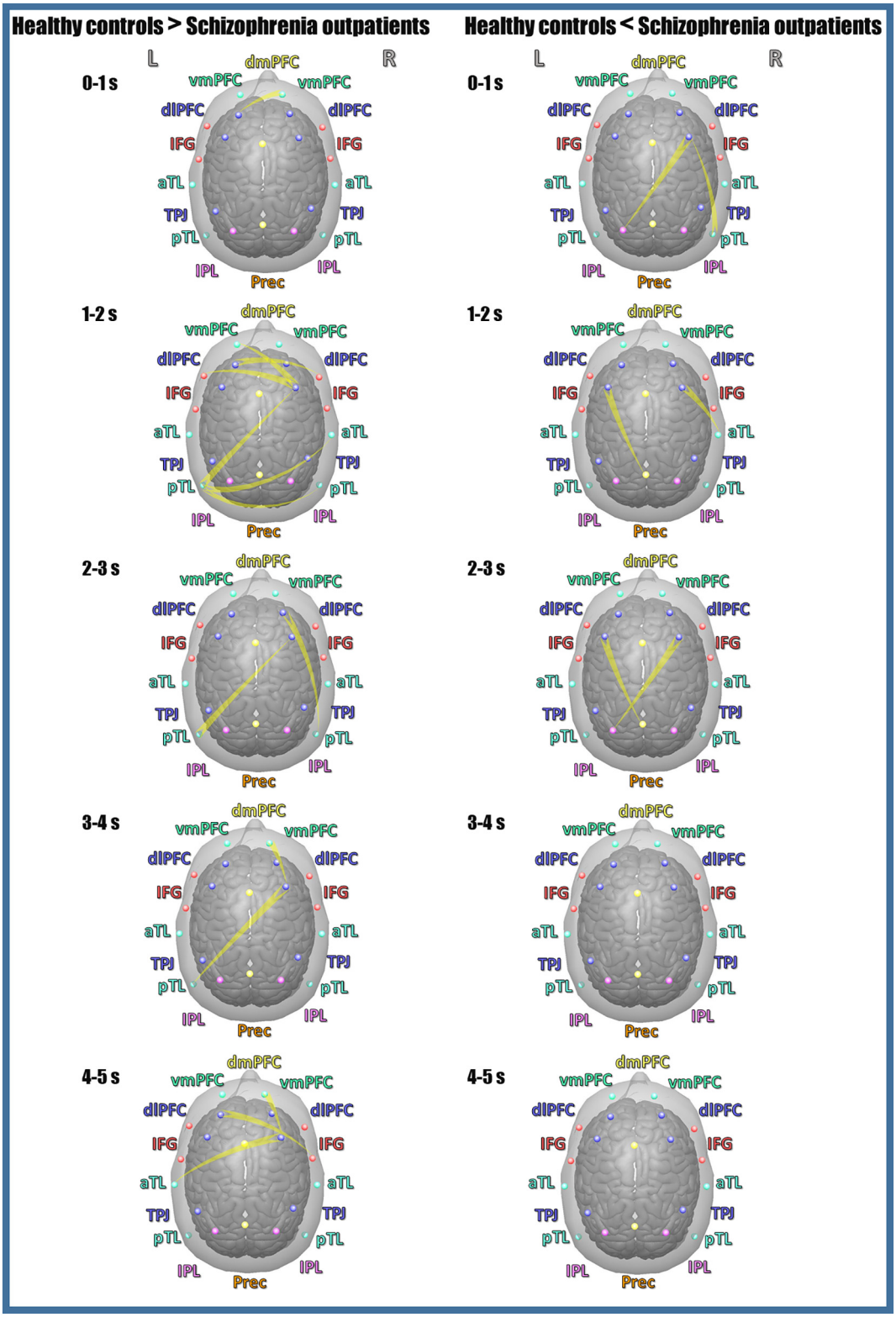

Fig. 1. Effective connectivity maps for conjunction analysis of incongruity detection contrast. Information flow in the humour-related neural circuit revealed by between-group contrasts presented in 5 epochs (0–1, 1–2, 2–3, 3–4, 4–5 s). Conjunction maps of effective connectivity for written and pictorial jokes during incongruity detection (ABS vs NEU). Arrows reflects the group differences in information flow (source → receiver). L – left hemisphere; R – right hemisphere; dmPFC – dorsomedial prefrontal cortex; vmPFC – ventromedial prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; IFG – inferior frontal gyrus; aTL – anterior temporal lobe; TPJ – temporoparietal junction; pTL – posterior temporal lobe; IPL – inferior parietal lobule; Prec – precuneus.

humour processing (FUN vs NEU). Finally, conjunction maps (the joint effects for both types of jokes) were created to reveal the prominent changes in effective connectivity beyond the modality context. To decrease the risk of false positives due to multiple comparisons, only directions whose p-level was ≤0.001 for at least one modality (i.e. written or pictorial jokes) were taken into account.

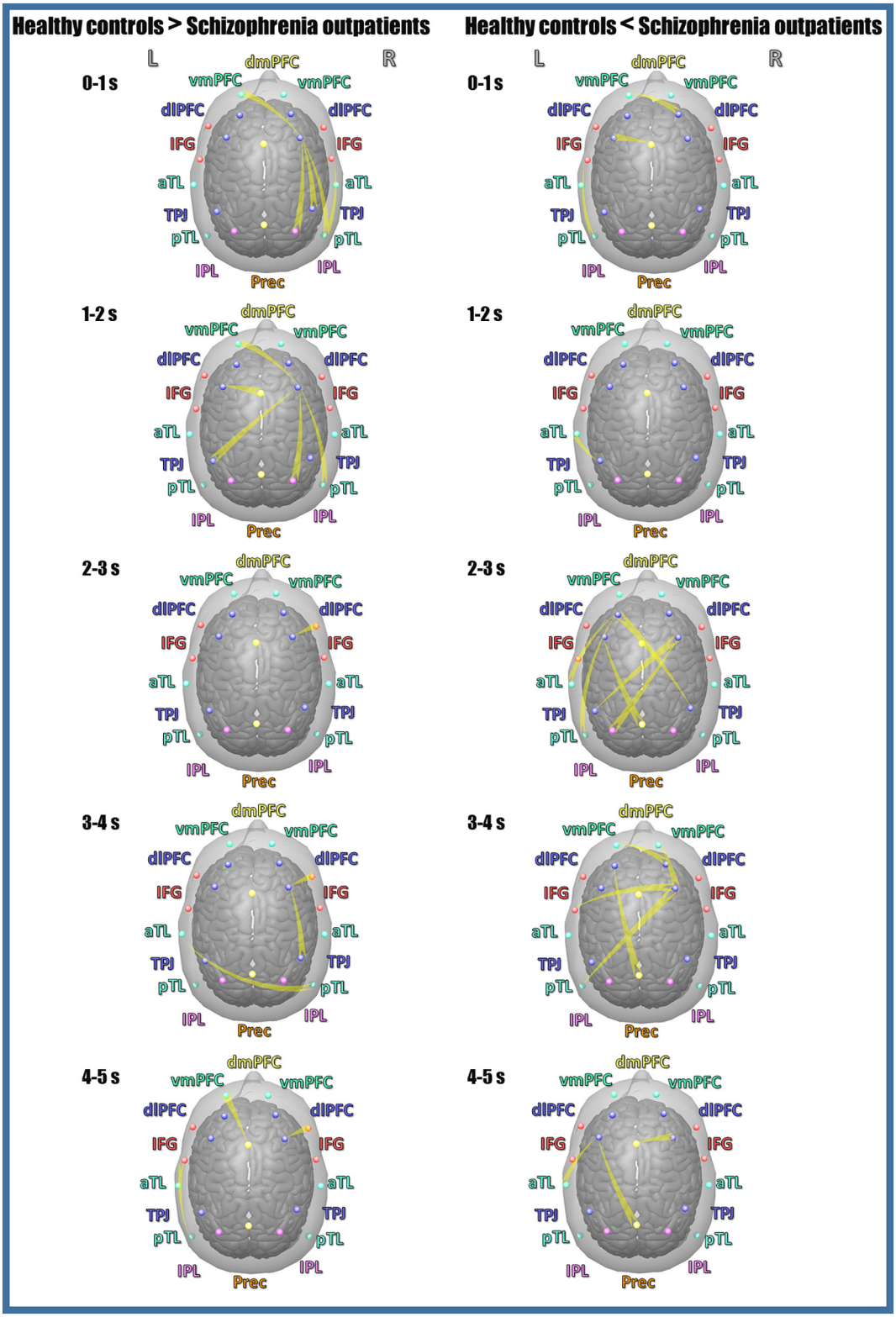

Fig. 2. Effective connectivity maps for conjunction analysis of incongruity resolution and elaboration contrast. Information flow in the humour-related neural circuit revealed by between-group contrasts presented in 5 epochs (0–1, 1–2, 2–3, 3–4, 4–5 s). Conjunction maps of effective connectivity for written and pictorial jokes during incongruity resolution and elaboration (FUN vs ABS). Arrows reflect the group differences in information flow (source → receiver). L – left hemisphere; R – right hemisphere; dmPFC – dorsomedial prefrontal cortex; vmPFC – ventromedial prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; IFG – inferior frontal gyrus; aTL – anterior temporal lobe; TPJ – temporoparietal junction; pTL – posterior temporal lobe; IPL – inferior parietal lobule; Prec – precuneus.

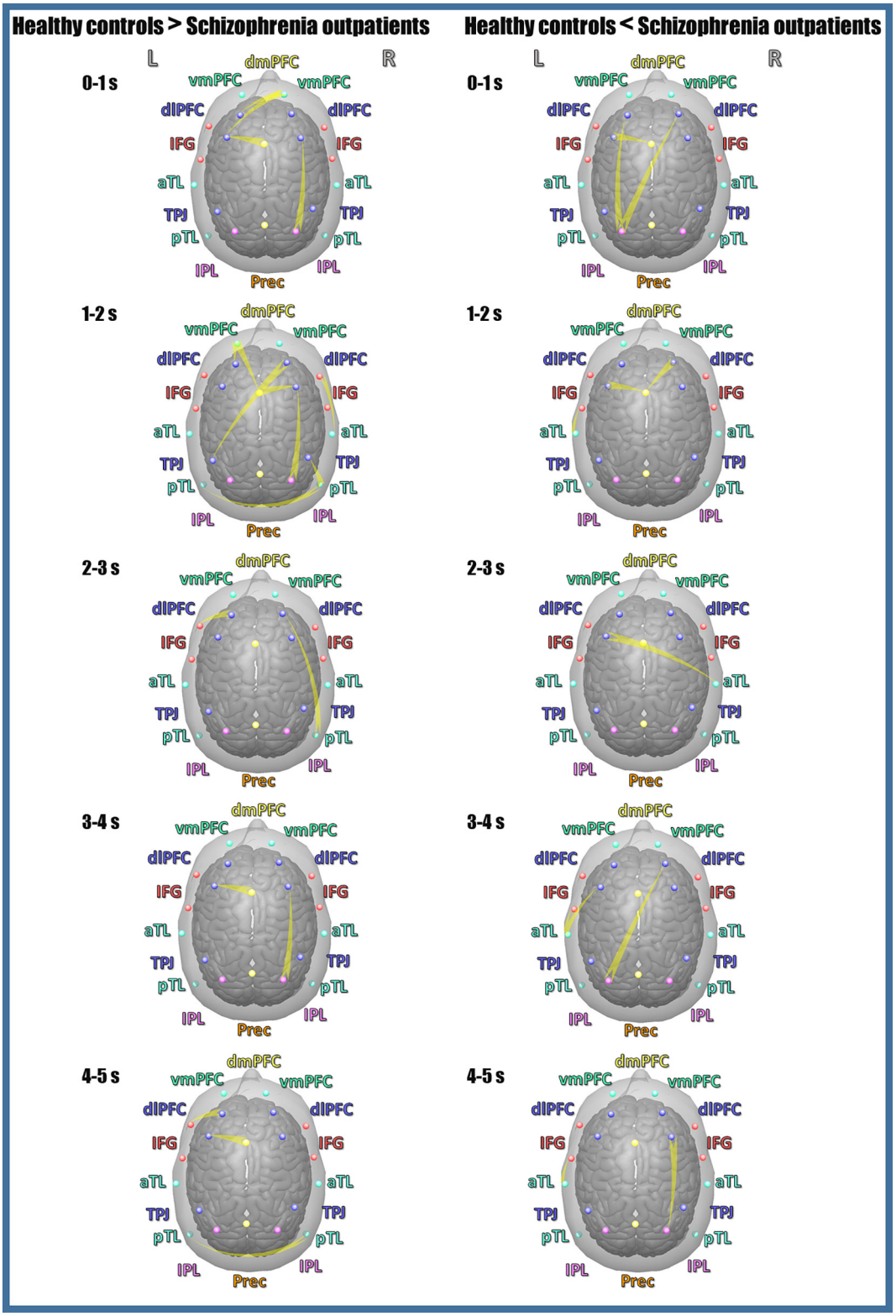

Fig. 3. Effective connectivity maps for conjunction analysis of complete humour processing contrast. Information flow in the humour-related neural circuit revealed by between-group contrasts presented in 5 epochs (0–1, 1–2, 2–3, 3–4, 4–5 s). Conjunction maps of effective connectivity for written and pictorial jokes during complete humour processing (FUN vs NEU). Arrows reflect the group differences in information flow (source → receiver). L – left hemisphere; R – right hemisphere; dmPFC – dorsomedial prefrontal cortex; vmPFC – ventromedial prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; IFG – inferior frontal gyrus; aTL – anterior temporal lobe; TPJ – temporoparietal junction; pTL – posterior temporal lobe; IPL – inferior parietal lobule; Prec – precuneus.

Table 3
DTF statistics for conjunction analysis of incongruity detection contrast.

Direction of information flow			Within-group effects of conditions: ABS vs NEU												Between-group Interaction effects					
ROIs	Electrodes	Time window (s)	Healthy controls (n = 40)						Schizophrenia outpatients (n = 40)											
			Stories			Cartoons			Stories			Cartoons			Stories			Cartoons		
			Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value
Healthy controls > schizophrenia outpatients																				
RvmPFC → LdlPFC	Fp2 → AF3	0–1	0.36 (0.23–0.49)	0.659	<0.001	0.20 (0.05–0.36)	0.494	0.008	−0.12 (−0.25 to −0.00)	0.500	0.051	−0.14 (−0.29–0.01)	0.384	0.079	−0.39 (−0.60 to −0.19)	0.344	<0.001	−0.34 (−0.54 to −0.13)	0.320	0.001
RdlPFC → LvmPFC	F4 → Fp1	1–2	0.40 (0.25–0.54)	0.561	<0.001	0.28 (0.12–0.44)	0.493	<0.001	0.01 (−0.15–0.18)	0.462	0.863	0.01 (−0.18–0.19)	0.318	0.944	−0.40 (−0.60 to −0.20)	0.317	<0.001	−0.28 (−0.50 to −0.07)	0.275	0.009
RdlPFC → LIFG	F4 → F7		−0.05 (−0.20–0.10)	0.536	0.550	0.47 (0.31–0.63)	0.497	<0.001	−0.46 (−0.61 to −0.30)	0.533	<0.001	0.13 (−0.05–0.30)	0.356	0.183	−0.36 (−0.56 to −0.16)	0.309	<0.001	−0.33 (−0.53 to −0.12)	0.290	0.002
LdlPFC → RIFG	AF3 → F8		−0.14 (−0.29–0.00)	0.604	0.059	0.21 (0.03–0.40)	0.375	0.019	−0.35 (−0.49 to −0.22)	0.635	<0.001	−0.23 (−0.38 to −0.07)	0.498	0.008	−0.26 (−0.46 to −0.05)	0.357	0.014	−0.42 (−0.64 to −0.20)	0.243	< 0.001
LpTL → RdlPFC	P7 → F4		0.40 (0.26–0.55)	0.590	<0.001	0.40 (0.23–0.56)	0.461	<0.001	−0.16 (−0.30 to −0.02)	0.575	0.037	0.01 (−0.16–0.17)	0.457	0.932	−0.33 (−0.52 to −0.14)	0.426	0.001	−0.22 (−0.43 to −0.01)	0.311	0.041
LpTL → RaTL	P7 → T8		0.27 (0.12–0.41)	0.562	<0.001	0.27 (0.10–0.44)	0.457	0.001	−0.12 (−0.25–0.02)	0.657	0.121	−0.16 (−0.33 to −0.00)	0.483	0.046	−0.30 (−0.48 to −0.12)	0.452	0.002	−0.32 (−0.53 to −0.11)	0.314	0.002
LpTL → RpTL	P7 → P8		0.31 (0.17–0.44)	0.614	<0.001	0.13 (−0.02–0.28)	0.596	0.090	−0.20 (−0.33 to −0.07)	0.657	0.004	−0.21 (−0.36 to −0.06)	0.467	0.007	−0.42 (−0.62 to −0.23)	0.340	<0.001	−0.32 (−0.53 to −0.11)	0.317	0.003
RdlPFC → RpTL	AF4 → P8	2–3	0.25 (0.10–0.39)	0.590	0.002	−0.05 (−0.20–0.10)	0.555	0.503	−0.24 (−0.38 to −0.10)	0.577	0.002	−0.28 (−0.44 to −0.13)	0.515	<0.001	−0.40 (−0.61 to −0.20)	0.300	<0.001	−0.24 (−0.45 to −0.04)	0.298	0.019
LpTL →	P7 → F4		0.27	0.590	<0.001	0.33	0.461	<0.001	−0.28	0.575	<0.001	−0.03	0.457	0.751	−0.35	0.426	<0.001	−0.26	0.311	0.014

RdlPFC			(0.12–0.41)			(0.16–0.50)			(−0.42 to −0.13)			(−0.19–0.14)			(−0.54 to −0.16)			(−0.47 to −0.05)		
RvmPFC → RdlPFC	Fp2 → F4	3–4	0.56 (0.41–0.71)	0.515	<0.001	-0.05 (−0.23–0.13)	0.400	0.592	−0.18 (−0.33 to −0.03)	0.562	0.025	−0.42 (−0.59 to −0.26)	0.513	<0.001	−0.62 (−0.82 to −0.42)	0.325	<0.001	−0.32 (−0.54 to −0.10)	0.275	0.003
RdlPFC → LpTL	F4 → P7		−0.03 (−0.18–0.12)	0.548	0.744	0.24 (0.07–0.41)	0.423	0.008	−0.29 (−0.43 to −0.14)	0.556	<0.001	−0.17 (−0.35–0.02)	0.353	0.073	−0.24 (−0.44 to −0.04)	0.346	0.025	−0.39 (−0.61 to −0.18)	0.237	< 0.001
RvmPFC → RdlPFC	Fp2 → F4	4–5	0.40 (0.23–0.56)	0.515	<0.001	−0.15 (−0.33–0.03)	0.400	0.095	−0.11 (−0.26–0.05)	0.562	0.187	−0.43 (−0.58 to −0.27)	0.513	<0.001	−0.47 (−0.68 to −0.26)	0.325	<0.001	−0.24 (−0.46 to −0.03)	0.275	0.024
RdlPFC → LaTL	F4 → T7		0.24 (0.10–0.38)	0.631	<0.001	-0.03 (−0.20–0.13)	0.483	0.701	−0.22 (−0.37 to −0.07)	0.607	0.004	−0.44 (−0.61 to −0.27)	0.460	<0.001	−0.41 (−0.62 to −0.19)	0.271	<0.001	−0.31 (−0.53 to −0.08)	0.232	0.007
LdlPFC → RIFG	AF3 → FC6		0.14 (−0.01–0.29)	0.601	0.067	0.10 (−0.07–0.27)	0.434	0.240	−0.11 (−0.25–0.04)	0.585	0.152	−0.31 (−0.46 to −0.16)	0.541	<0.001	−0.22 (−0.44 to −0.00)	0.252	0.049	−0.37 (−0.58 to −0.16)	0.281	< 0.001
Healthy controls < schizophrenia outpatients																			
RdlPFC → LIPL	F4 → P3	0–1	−0.36 (−0.51 to −0.21)	0.575	<0.001	−0.07 (−0.23–0.10)	0.452	0.410	0.15 (−0.02–0.32)	0.491	0.083	0.36 (0.18–0.53)	0.405	<0.001	0.48 (0.27–0.69)	0.349	<0.001	0.32 (0.11–0.54)	0.280	0.002
RpTL → RdlPFC	P8 → F4		0.01 (−0.17–0.20)	0.391	0.879	0.24 (0.05–0.42)	0.335	0.014	0.39 (0.23–0.54)	0.573	<0.001	0.49 (0.32–0.67)	0.364	<0.001	0.38 (0.16–0.60)	0.330	<0.001	0.32 (0.10–0.53)	0.246	0.003
RdlPFC → RaTL	F4 → T8	1–2	−0.17 (−0.31 to −0.02)	0.566	0.040	−0.23 (−0.39 to −0.06)	0.450	0.008	0.14 (−0.00–0.29)	0.594	0.065	0.22 (0.06–0.38)	0.490	0.009	0.21 (0.01–0.42)	0.294	0.059	0.38 (0.17–0.60)	0.269	< 0.001
LdlPFC → Prec	F3 → Pz		0.17 (0.02–0.32)	0.568	0.032	0.03 (−0.13–0.19)	0.470	0.703	0.34 (0.20–0.49)	0.596	<0.001	0.43 (0.26–0.60)	0.452	<0.001	0.27 (0.07–0.47)	0.351	0.012	0.39 (0.18–0.60)	0.277	< 0.001
RdlPFC → LIPL	F4 → P3	2–3	−0.36 (−0.50 to −0.22)	0.575	<0.001	−0.21 (−0.37 to −0.04)	0.452	0.012	0.05 (−0.11–0.20)	0.491	0.579	0.10 (−0.07–0.27)	0.405	0.240	0.38 (0.19–0.58)	0.349	<0.001	0.22 (0.01–0.42)	0.280	0.040
LdlPFC → Prec	F3 → Pz		0.10 (−0.05–0.25)	0.568	0.181	−0.13 (−0.30–0.03)	0.470	0.120	0.31 (0.17–0.45)	0.596	<0.001	0.30 (0.13–0.46)	0.452	<0.001	0.31 (0.11–0.52)	0.351	0.003	0.36 (0.15–0.58)	0.277	0.001

List of Regions of Interest (ROIs) and directions of electrode pairs (source → receiver) revealed by conjunction analysis of written and pictorial joke processing. Statistics for incongruity detection contrast presented as within-group and within-modality Standardized Beta Coefficients with Confidence Intervals in appropriate epochs as well as between-group differences (i.e. interaction group effects). ROIs definition: L, left; R, right; ventromedial prefrontal cortex (vmPFC, BA 10); dorsomedial prefrontal cortex (dmPFC BA 8/32); dorsolateral prefrontal cortex (dlPFC, BA 9); inferior frontal gyrus (IFG, BA 44/45); anterior temporal lobe (aTL, BA 21/22); posterior temporal lobe (pTL, BA 37); temporoparietal junction (TPJ, BA 40); inferior parietal lobule (IPL, BA 39); precuneus (Prec, BA 7/31).

Table 4
DTF statistics for conjunction analysis of incongruity resolution and elaboration contrast.

Direction of information flow			Within-group effects of conditions: FUN vs ABS												Between-group interaction effects					
ROIs	Electrodes	Time window (s)	Healthy controls (n = 40)						Schizophrenia outpatients (n = 40)											
			Stories			Cartoons			Stories			Cartoons			Stories			Cartoons		
			Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value	Standardized beta coefficients (confidence intervals)	R2	P-value
Healthy controls > schizophrenia outpatients																				
LvmPFC → RdlPFC	Fp1 → F4	0–1	0.25 (0.10–0.40)	0.578	0.001	0.26 (0.08–0.44)	0.406	0.005	−0.32 (−0.47 to −0.17)	0.572	<0.001	−0.06 (−0.22–0.10)	0.492	0.451	−0.51 (−0.71 to −0.30)	0.315	<0.001	−0.27 (−0.47 to −0.06)	0.311	0.013
RIPL → RdlPFC	P4 → F4		0.47 (0.30–0.64)	0.432	<0.001	0.12 (−0.06–0.30)	0.339	0.187	−0.39 (−0.55 to −0.22)	0.510	<0.001	−0.15 (−0.33–0.03)	0.328	0.090	−0.71 (−0.92 to −0.51)	0.362	<0.001	−0.22 (−0.42 to −0.01)	0.261	0.041
RpTL → RdlPFC	P8 → F4		0.24 (0.06–0.43)	0.391	0.009	−0.14 (−0.32–0.04)	0.335	0.147	−0.42 (−0.57 to −0.26)	0.573	<0.001	−0.44 (−0.62 to −0.26)	0.364	<0.001	−0.52 (−0.74 to −0.31)	0.330	<0.001	−0.37 (−0.59 to −0.15)	0.246	<0.001
RpTL → RIFG	P8 → FC6		0.40 (0.24–0.56)	0.475	<0.001	0.07 (−0.11–0.24)	0.389	0.469	−0.27 (−0.43 to −0.12)	0.562	<0.001	−0.20 (−0.39 to −0.01)	0.354	0.028	−0.59 (−0.80 to −0.38)	0.304	<0.001	−0.24 (−0.46 to −0.02)	0.264	0.035
RTPJ → RdlPFC	CP6 → F4		0.21 (0.05–0.36)	0.515	0.015	0.49 (0.32–0.65)	0.447	<0.001	−0.18 (−0.34 to −0.02)	0.521	0.029	0.04 (−0.15–0.23)	0.317	0.652	−0.36 (−0.57 to −0.15)	0.322	<0.001	−0.44 (−0.65 to −0.23)	0.265	<0.001
LvmPFC → RdlPFC	Fp1 → F4	1–2	0.31 (0.16–0.45)	0.578	<0.001	0.28 (0.10–0.45)	0.406	0.003	−0.36 (−0.50 to −0.21)	0.572	<0.001	−0.14 (−0.30–0.03)	0.492	0.098	−0.56 (−0.76 to −0.36)	0.315	<0.001	−0.33 (−0.55 to −0.12)	0.311	0.002
RIPL → RdlPFC	P4 → F4		0.38 (0.22–0.55)	0.432	<0.001	0.38 (0.19–0.56)	0.339	<0.001	−0.53 (−0.68 to −0.37)	0.510	<0.001	−0.07 (−0.25–0.11)	0.328	0.440	−0.76 (−0.95 to −0.56)	0.362	<0.001	−0.32 (−0.53 to −0.10)	0.261	0.003
RpTL → RdlPFC	P8 → F4		−0.07 (−0.24–0.10)	0.391	0.437	0.21 (0.03–0.39)	0.335	0.028	−0.65 (−0.79 to −0.51)	0.573	<0.001	−0.15 (−0.33–0.02)	0.364	0.087	−0.47 (−0.67 to −0.27)	0.330	<0.001	−0.26 (−0.47 to −0.04)	0.246	0.021
LTPJ → RdlPFC	CP5 → F4		0.43 (0.28–0.58)	0.539	<0.001	0.02 (−0.14–0.19)	0.420	0.781	−0.03 (−0.19–0.12)	0.507	0.685	−0.27 (−0.45 to −0.08)	0.322	0.006	−0.34 (−0.54 to −0.14)	0.307	0.001	−0.25 (−0.47 to −0.04)	0.221	0.023
dmPFC → LdlPFC	Fz → F3		−0.01 (−0.15–0.14)	0.591	0.928	0.30 (0.15–0.45)	0.522	<0.001	−0.44 (−0.56 to −0.31)	0.678	<0.001	0.04 (−0.13–0.21)	0.425	0.633	−0.45 (−0.64 to −0.27)	0.413	<0.001	−0.24 (−0.45 to −0.03)	0.292	0.024
RIFG → RdlPFC	F8 → F4	2–3	0.19 (0.04–0.35)	0.532	0.023	−0.05 (−0.21–0.11)	0.511	0.531	−0.20 (−0.35 to −0.04)	0.507	0.023	−0.46 (−0.61 to −0.31)	0.526	<0.001	−0.34 (−0.54 to −0.13)	0.294	0.004	−0.43 (−0.63 to −0.22)	0.282	<0.001
RIFG → RdlPFC	F8 → F4	3–4	0.27 (0.12–0.42)	0.532	0.002	−0.02 (−0.17–0.14)	0.511	0.844	−0.17 (−0.33 to −0.00)	0.507	0.055	−0.47 (−0.62 to −0.31)	0.526	<0.001	−0.33 (−0.54 to −0.12)	0.294	0.004	−0.50 (−0.71 to −0.29)	0.282	<0.001
RpTL → LaTL	P8 → T7		−0.12 (−0.27–0.02)	0.572	0.103	0.51 (0.35–0.68)	0.469	<0.001	−0.40 (−0.55 to −0.26)	0.564	<0.001	−0.04 (−0.24–0.15)	0.286	0.662	−0.23 (−0.43 to −0.03)	0.302	0.032	−0.45 (−0.67 to −0.23)	0.221	<0.001
RTPJ → RdlPFC	CP6 → F4		0.32 (0.16–0.47)	0.515	<0.001	0.27 (0.11–0.44)	0.447	0.001	−0.18 (−0.34 to −0.03)	0.521	0.025	−0.07 (−0.26–0.11)	0.317	0.459	−0.43 (−0.63 to −0.23)	0.322	<0.001	−0.34 (−0.54 to −0.13)	0.265	0.002
RIFG → RdlPFC	F8 → F4	4–5	0.20 (0.03–0.37)	0.532	0.019	−0.09 (−0.24–0.07)	0.511	0.276	−0.15 (−0.32–0.02)	0.507	0.081	−0.44 (−0.60 to −0.28)	0.526	<0.001	−0.31 (−0.54 to −0.08)	0.294	0.007	−0.40 (−0.61 to −0.19)	0.282	<0.001
LvmPFC →	Fp1 → Fz		0.24 (0.09–0.39)	0.584	0.001	0.22 (0.06–0.38)	0.503	0.007	−0.23 (−0.38 to	0.630	0.002	−0.11 (−0.26–0.05)	0.520	0.180	−0.38 (−0.59 to	0.303	<0.001	−0.28 (−0.49 to	0.328	0.007

dmPFC									−0.09)					−0.16)			−0.08)		
LIFG → LpTL	FC5 → P7		0.49 (0.35–0.64)	0.581	<0.001	0.14 (−0.02–0.30)	0.475	0.082	−0.03 (−0.20–0.13)	0.524	0.687	−0.10 (−0.26–0.06)	0.468	0.232	−0.47 (−0.67 to −0.26)	0.359	<0.001	−0.22 (−0.43 to −0.01)	0.257	0.041
Healthy controls < schizophrenia outpatients																				
RdlPFC → LvmPFC	AF4 → Fp1	0–1	−0.25 (−0.42 to −0.09)	0.508	0.002	−0.18 (−0.34 to −0.01)	0.461	0.045	0.14 (−0.01–0.29)	0.562	0.073	0.34 (0.17–0.51)	0.413	<0.001	0.34 (0.13–0.55)	0.319	0.002	0.46 (0.25–0.67)	0.262	<0.001
LdlPFC → dmPFC	F3 → Fz		−0.07 (−0.22–0.07)	0.632	0.298	−0.16 (−0.32–0.01)	0.423	0.064	0.21 (0.07–0.35)	0.618	0.004	−0.02 (−0.19–0.16)	0.473	0.854	0.38 (0.16–0.60)	0.294	<0.001	0.29 (0.08–0.51)	0.269	0.008
LpTL → LIFG	P7 → FC5		−0.18 (−0.34 to −0.01)	0.467	0.042	0.06 (−0.12–0.23)	0.368	0.518	0.17 (0.02–0.32)	0.587	0.024	0.50 (0.34–0.66)	0.496	<0.001	0.32 (0.12–0.52)	0.345	0.002	0.47 (0.27–0.68)	0.283	<0.001
LaTL → LTPJ	T7 → CP5	1–2	0.11 (−0.01–0.24)	0.687	0.088	0.05 (−0.10–0.21)	0.523	0.498	0.33 (0.22–0.44)	0.766	<0.001	0.36 (0.22–0.50)	0.623	<0.001	0.27 (0.08–0.46)	0.431	0.007	0.35 (0.16–0.54)	0.408	<0.001
LdlPFC → RTPJ	AF3 → CP6	2–3	−0.29 (−0.43 to −0.14)	0.593	<0.001	0.05 (−0.12–0.21)	0.459	0.585	0.15 (0.01–0.29)	0.636	0.031	0.34 (0.19–0.50)	0.527	<0.001	0.39 (0.18–0.60)	0.332	<0.001	0.30 (0.08–0.52)	0.253	0.008
LpTL → LdlPFC	P7 → AF3		−0.17 (−0.30 to −0.03)	0.627	0.019	−0.10 (−0.26–0.05)	0.488	0.210	0.37 (0.24–0.50)	0.635	<0.001	0.16 (−0.01–0.32)	0.457	0.058	0.48 (0.29–0.66)	0.440	<0.001	0.20 (−0.00–0.41)	0.325	0.055
LaTL → LdlPFC	T7 → AF3		−0.08 (−0.23–0.06)	0.567	0.291	−0.12 (−0.28–0.04)	0.494	0.153	0.19 (0.06–0.33)	0.638	0.006	0.53 (0.38–0.68)	0.544	<0.001	0.21 (0.01–0.40)	0.364	0.047	0.63 (0.43–0.83)	0.389	<0.001
LIPL → RdlPFC	P3 → F4		−0.25 (−0.40 to −0.10)	0.540	0.001	−0.40 (−0.58 to −0.22)	0.368	<0.001	0.06 (−0.10–0.21)	0.527	0.478	0.28 (0.10–0.45)	0.368	0.003	0.23 (0.03–0.42)	0.379	0.022	0.54 (0.33–0.76)	0.263	<0.001
RdlPFC → LTPJ	F4 → CP5		−0.29 (−0.43 to −0.14)	0.589	<0.001	−0.19 (−0.35 to −0.03)	0.487	0.024	0.17 (0.02–0.32)	0.509	0.050	0.10 (−0.07–0.27)	0.410	0.258	0.41 (0.20–0.61)	0.290	<0.001	0.23 (0.01–0.45)	0.237	0.041
Prec → LdlPFC	Pz → F3		−0.45 (−0.60 to −0.30)	0.555	<0.001	0.04 (−0.14–0.22)	0.356	0.689	0.10 (−0.05–0.25)	0.564	0.207	0.37 (0.20–0.53)	0.490	<0.001	0.46 (0.26–0.66)	0.345	<0.001	0.35 (0.14–0.56)	0.298	0.001
RdlPFC → LvmPFC	AF4 → Fp1	3–4	−0.38 (−0.53 to −0.22)	0.508	<0.001	0.20 (0.03–0.36)	0.461	0.024	0.01 (−0.14–0.16)	0.562	0.884	0.59 (0.42–0.76)	0.413	<0.001	0.27 (0.07–0.47)	0.319	0.011	0.42 (0.21–0.64)	0.262	<0.001
RdlPFC → RvmPFC	F4 → Fp2		−0.21 (−0.36 to −0.06)	0.531	0.012	−0.14 (−0.31–0.04)	0.395	0.127	0.30 (0.14–0.45)	0.499	<0.001	0.21 (0.02–0.41)	0.264	0.033	0.41 (0.22–0.61)	0.34	<0.001	0.28 (0.06–0.50)	0.169	0.013
RdlPFC → LIFG	F4 → FC5		−0.30 (−0.44 to −0.16)	0.587	<0.001	−0.19 (−0.36 to −0.01)	0.435	0.031	0.37 (0.23–0.51)	0.619	<0.001	0.25 (0.08–0.43)	0.399	0.005	0.62 (0.44–0.81)	0.29	<0.001	0.35 (0.13–0.58)	0.237	0.002
RdlPFC → LpTL	F4 → P7		−0.10 (−0.25–0.05)	0.548	0.213	−0.23 (−0.40 to −0.06)	0.423	0.009	0.37 (0.23–0.52)	0.556	<0.001	0.11 (−0.08–0.29)	0.353	0.246	0.39 (0.19–0.58)	0.34	<0.001	0.30 (0.09–0.52)	0.237	0.007
Prec → LdlPFC	Pz → AF3		−0.32 (−0.47 to −0.17)	0.575	<0.001	−0.18 (−0.35 to −0.01)	0.391	0.036	−0.00 (−0.16–0.15)	0.523	0.975	0.29 (0.13–0.46)	0.445	<0.001	0.26 (0.05–0.48)	0.272	0.017	0.41 (0.21–0.61)	0.314	<0.001
RdlPFC → dmPFC	F4 → Fz	4–5	−0.22 (−0.37 to −0.07)	0.563	0.005	−0.02 (−0.18–0.14)	0.484	0.829	0.19 (0.02–0.36)	0.475	0.031	0.27 (0.10–0.43)	0.476	0.002	0.38 (0.16–0.60)	0.290	<0.001	0.24 (0.02–0.45)	0.271	0.033
Prec → LdlPFC	Pz → F3		−0.32 (−0.48 to −0.17)	0.555	<0.001	−0.16 (−0.34–0.02)	0.356	0.078	−0.05 (−0.20–0.10)	0.564	0.512	0.35 (0.18–0.51)	0.490	<0.001	0.24 (0.03–0.44)	0.345	0.025	0.44 (0.23–0.66)	0.298	<0.001
LaTL → LdlPFC	T7 → F3		0.06 (−0.08–0.21)	0.585	0.406	−0.17 (−0.34–0.00)	0.473	0.052	0.20 (0.06–0.34)	0.644	0.006	0.28 (0.12–0.43)	0.503	<0.001	0.24 (0.05–0.43)	0.426	0.015	0.40 (0.18–0.62)	0.243	<0.001

List of Regions of Interest (ROIs) and directions of electrode pair (source → receiver) revealed by conjunction analysis of written and pictorial joke processing. Statistics for incongruity resolution and elaboration contrast presented as within-group and within-modality mean DTF beta values with confidence intervals in appropriate epochs as well as between-group differences (i.e. interaction with group) effects. ROIs definition: L, left; R, right; ventromedial prefrontal cortex (vmPFC, BA 10); dorsomedial prefrontal cortex (dmPFC BA 8/32); dorsolateral prefrontal cortex (dlPFC, BA 9); inferior frontal gyrus (IFG, BA 44/45); anterior temporal lobe (aTL, BA 21/22); posterior temporal lobe (pTL, BA 37); temporoparietal junction (TPJ, BA 40); inferior parietal lobule (IPL, BA 39); precuneus (Prec, BA 7/31).

Table 5
DTF statistics for conjunction analysis of complete humour processing contrast.

Direction of information flow			Within-group effects of conditions: FUN vs NEU												Between-group Interaction effects					
ROIs	Electrodes	Time window (s)	Healthy controls (n = 40)						Schizophrenia outpatients (n = 40)											
			Stories			Cartoons			Stories			Cartoons			Stories			Cartoons		
			Standardized beta coefficients (with confidence intervals)	R2	P-value	Standardized beta coefficients (with confidence intervals)	R2	P-value	Standardized beta coefficients (with confidence intervals)	R2	P-value	Standardized beta coefficients (with confidence intervals)	R2	P-value	Standardized beta coefficients (with confidence intervals)	R2	P-value	Standardized beta coefficients (with confidence intervals)	R2	P-value
Healthy controls > schizophrenia outpatients																				
RvmPFC → LdlPFC	Fp2 → AF3	0–1	0.21 (0.07–0.34)	0.659	0.002	0.11 (−0.04–0.27)	0.533	0.147	−0.30 (−0.43 to −0.17)	0.704	<0.001	−0.19 (−0.34 to −0.03)	0.522	0.019	−0.47 (−0.67 to −0.26)	0.344	<0.001	−0.31 (−0.52 to −0.10)	0.320	0.003
RvmPFC → LdlPFC	Fp2 → F3		0.21 (0.06–0.36)	0.597	0.007	0.16 (−0.00–0.32)	0.489	0.060	−0.35 (−0.49 to −0.22)	0.679	<0.001	−0.16 (−0.32 to −0.00)	0.513	0.046	−0.47 (−0.67 to −0.27)	0.378	<0.001	−0.32 (−0.53 to −0.11)	0.282	0.003
dmPFC → LdlPFC	Fz → F3		0.05 (−0.09–0.20)	0.591	0.486	0.20 (0.04–0.36)	0.522	0.011	−0.51 (−0.64 to −0.38)	0.678	<0.001	−0.08 (−0.25–0.09)	0.425	0.368	−0.49 (−0.68 to −0.29)	0.413	<0.001	−0.26 (−0.47 to −0.05)	0.292	0.015
RIPL → RdlPFC	P4 → F4		0.34 (0.16–0.51)	0.432	<0.001	−0.01 (−0.19–0.17)	0.339	0.879	−0.34 (−0.50 to −0.17)	0.510	<0.001	−0.32 (−0.50 to −0.14)	0.328	<0.001	−0.54 (−0.75 to −0.34)	0.362	<0.001	−0.23 (−0.44 to −0.02)	0.261	0.026
LvmPFC → LdlPFC	Fp1 → AF3	1–2	0.29 (0.16–0.42)	0.662	<0.001	0.17 (0.01–0.34)	0.482	0.031	−0.21 (−0.36 to −0.06)	0.565	0.006	−0.21 (−0.38 to −0.04)	0.426	0.017	−0.39 (−0.60 to −0.18)	0.296	<0.001	−0.32 (−0.53 to −0.10)	0.281	0.003
LvmPFC → dmPFC	Fp1 → Fz		0.09 (−0.06–0.23)	0.584	0.258	0.17 (0.00–0.33)	0.503	0.042	−0.14 (−0.28 to −0.01)	0.630	0.056	−0.22 (−0.38 to −0.06)	0.520	0.007	−0.21 (−0.42 to −0.00)	0.303	0.054	−0.36 (−0.57 to −0.15)	0.328	<0.001
RdlPFC → LTPJ	AF4 → CP5		0.08 (−0.07–0.22)	0.570	0.305	0.22 (0.06–0.39)	0.453	0.010	−0.36 (−0.50 to −0.23)	0.632	<0.001	−0.11 (−0.27–0.04)	0.521	0.173	−0.39 (−0.60 to −0.18)	0.289	<0.001	−0.28 (−0.49 to −0.06)	0.231	0.016
dmPFC → RdlPFC	Fz → F4		0.16 (0.01–0.30)	0.576	0.038	0.32 (0.15–0.48)	0.466	<0.001	−0.29 (−0.44 to −0.15)	0.570	<0.001	0.05 (−0.11–0.22)	0.417	0.535	−0.37 (−0.55 to −0.18)	0.441	<0.001	−0.25 (−0.46 to −0.05)	0.312	0.017
RIPL → RdlPFC	P4 → F4		0.22 (0.05–0.39)	0.432	0.010	0.03 (−0.15–0.21)	0.339	0.749	−0.53 (−0.69 to −0.38)	0.510	<0.001	−0.25 (−0.42 to −0.07)	0.328	0.006	−0.62 (−0.82 to −0.43)	0.362	<0.001	−0.22 (−0.43 to −0.01)	0.261	0.036
RIFG → RaTL	F8 → T8		0.12 (0.00–0.25)	0.696	0.050	0.29 (0.16–0.43)	0.617	<0.001	−0.24 (−0.39 to −0.10)	0.575	0.001	0.13 (−0.04–0.30)	0.434	0.136	−0.32 (−0.51 to −0.13)	0.385	0.001	−0.24 (−0.44 to −0.04)	0.347	0.018
RpTL → RTPJ	P8 → CP6		0.07 (−0.07–0.21)	0.588	0.364	0.06 (−0.08–0.20)	0.595	0.444	−0.20 (−0.34 to −0.06)	0.606	0.007	−0.35 (−0.52 to −0.19)	0.484	<0.001	−0.22 (−0.42 to −0.01)	0.298	0.048	−0.34 (−0.55 to −0.14)	0.314	0.001
RpTL → LpTL	P8 → P7		0.30 (0.15–0.45)	0.538	<0.001	0.17 (0.01–0.33)	0.479	0.038	−0.02 (−0.19–0.14)	0.439	0.777	−0.27 (−0.43 to −0.11)	0.485	<0.001	−0.23 (−0.44 to −0.02)	0.256	0.034	−0.41 (−0.61 to −0.20)	0.336	<0.001
LdlPFC → LIFG	AF3 → F7	2–3	0.22 (0.07–0.38)	0.520	0.007	0.29 (0.13–0.45)	0.478	<0.001	−0.31 (−0.44 to −0.18)	0.647	<0.001	−0.05 (−0.22–0.11)	0.475	0.542	−0.43 (−0.64 to −0.21)	0.237	<0.001	−0.28 (−0.50 to −0.06)	0.181	0.014
RpTL → RdlPFC	P8 → AF4		0.07 (−0.08–0.22)	0.529	0.401	0.05 (−0.15–0.24)	0.290	0.646	−0.32 (−0.47 to	0.562	<0.001	−0.30 (−0.48 to	0.371	0.001	−0.35 (−0.54 to	0.351	<0.001	−0.30 (−0.52 to	0.227	0.009

									−0.18)			−0.12)			−0.15)			−0.07)		
RIPL → RdlPFC	P4 → F4	3–4	0.19 (0.02–0.35)	0.432	0.029	−0.03 (−0.21–0.15)	0.339	0.757	−0.45 (−0.61 to −0.30)	0.510	<0.001	−0.46 (−0.64 to −0.28)	0.328	<0.001	−0.52 (−0.71 to −0.32)	0.362	<0.001	−0.34 (−0.55 to −0.13)	0.261	0.001
dmPFC → LdlPFC	Fz → F3		−0.05 (−0.19–0.09)	0.591	0.520	0.23 (0.08–0.39)	0.522	0.003	−0.40 (−0.52 to −0.27)	0.678	<0.001	−0.23 (−0.40 to −0.06)	0.425	0.009	−0.28 (−0.47 to −0.09)	0.413	0.005	−0.41 (−0.62 to −0.20)	0.292	<0.001
LdlPFC → LIFG	AF3 → F7	4–5	0.50 (0.34–0.66)	0.520	<0.001	0.04 (−0.12–0.19)	0.478	0.665	−0.32 (−0.45 to −0.18)	0.647	<0.001	−0.26 (−0.42 to −0.09)	0.475	0.002	−0.61 (−0.83 to −0.38)	0.237	<0.001	−0.24 (−0.46 to −0.01)	0.181	0.038
dmPFC → LdlPFC	Fz → F3		0.02 (−0.12–0.17)	0.591	0.740	0.16 (0.01–0.32)	0.522	0.038	−0.37 (−0.51 to −0.24)	0.678	<0.001	−0.16 (−0.33–0.00)	0.425	0.065	−0.35 (−0.54 to −0.15)	0.413	<0.001	−0.30 (−0.50 to −0.09)	0.292	0.005
RpTL → LpTL	P8 → P7		0.24 (0.09–0.40)	0.538	0.002	0.21 (0.05–0.37)	0.479	0.010	−0.06 (−0.23–0.10)	0.439	0.446	−0.23 (−0.39 to −0.07)	0.485	0.005	−0.25 (−0.46 to −0.03)	0.256	0.023	−0.40 (−0.60 to −0.19)	0.336	<0.001
Healthy controls < schizophrenia outpatients																				
LdlPFC → dmPFC	F3 → Fz	0–1	−0.32 (−0.46 to −0.18)	0.632	<0.001	−0.32 (−0.48 to −0.15)	0.423	<0.001	0.24 (0.10–0.38)	0.618	<0.001	−0.06 (−0.23–0.11)	0.473	0.502	0.56 (0.35–0.78)	0.294	<0.001	0.28 (0.07–0.49)	0.269	0.011
LIPL → LdlPFC	P3 → AF3		−0.49 (−0.65 to −0.34)	0.558	<0.001	−0.39 (−0.57 to −0.21)	0.370	<0.001	0.13 (−0.02–0.27)	0.607	0.099	−0.01 (−0.19–0.16)	0.393	0.870	0.52 (0.33–0.71)	0.436	<0.001	0.25 (0.04–0.45)	0.329	0.017
LIPL → RdlPFC	P3 → AF4		−0.29 (−0.44 to −0.14)	0.548	<0.001	−0.41 (−0.59 to −0.22)	0.337	<0.001	0.05 (−0.10–0.20)	0.598	0.512	0.15 (−0.02–0.32)	0.404	0.090	0.30 (0.11–0.50)	0.377	0.003	0.40 (0.19–0.61)	0.305	<0.001
RdlPFC → dmPFC	AF4 → Fz	1–2	−0.07 (−0.21–0.08)	0.569	0.384	−0.24 (−0.40 to −0.09)	0.548	0.002	0.23 (0.09–0.38)	0.577	0.003	0.26 (0.10–0.43)	0.474	0.002	0.21 (0.00–0.41)	0.32	0.053	0.38 (0.18–0.58)	0.320	<0.001
LdlPFC → dmPFC	F3 → Fz		−0.20 (−0.33 to −0.06)	0.632	0.005	−0.19 (−0.35 to −0.03)	0.423	0.027	0.15 (0.01–0.29)	0.618	0.038	0.05 (−0.12–0.22)	0.473	0.562	0.36 (0.15–0.57)	0.29	0.001	0.24 (0.03–0.45)	0.269	0.025
LaTL → LIFG	T7 → FC5		−0.17 (−0.30 to −0.05)	0.709	0.005	0.06 (−0.09–0.21)	0.575	0.429	0.21 (0.09–0.34)	0.697	<0.001	0.26 (0.13–0.40)	0.635	<0.001	0.35 (0.16–0.55)	0.39	<0.001	0.28 (0.07–0.48)	0.349	0.007
LdlPFC → RaTL	F3 → T8	2–3	−0.15 (−0.30 to −0.01)	0.566	0.050	−0.27 (−0.43 to −0.11)	0.503	<0.001	0.44 (0.31–0.57)	0.632	<0.001	0.00 (−0.17–0.17)	0.481	0.980	0.55 (0.34–0.75)	0.29	<0.001	0.23 (0.01–0.46)	0.244	0.034
LaTL → LIFG	T7 → FC5	3–4	−0.25 (−0.37 to −0.13)	0.709	<0.001	0.14 (−0.01–0.29)	0.575	0.065	0.33 (0.21–0.46)	0.697	<0.001	0.38 (0.25–0.52)	0.635	<0.001	0.51 (0.31–0.70)	0.39	<0.001	0.26 (0.06–0.46)	0.349	0.012
LaTL → LdlPFC	T7 → F3		0.02 (−0.12–0.16)	0.585	0.788	−0.01 (−0.18–0.17)	0.473	0.934	0.32 (0.18–0.46)	0.644	<0.001	0.18 (0.01–0.34)	0.503	0.029	0.37 (0.18–0.55)	0.426	<0.001	0.24 (0.02–0.47)	0.243	0.030
LIPL → RdlPFC	P3 → AF4		−0.36 (−0.51 to −0.21)	0.548	<0.001	−0.36 (−0.55 to −0.17)	0.337	<0.001	−0.12 (−0.26–0.02)	0.598	0.120	0.17 (0.00–0.34)	0.404	0.051	0.21 (0.02–0.40)	0.377	0.042	0.38 (0.17–0.59)	0.305	<0.001
LaTL → LIFG	T7 → FC5	4–5	−0.15 (−0.28 to −0.03)	0.709	0.016	0.04 (−0.10–0.19)	0.575	0.565	0.41 (0.28–0.53)	0.697	<0.001	0.32 (0.19–0.46)	0.635	<0.001	0.58 (0.38–0.78)	0.391	<0.001	0.28 (0.08–0.49)	0.349	0.006
RdlPFC → RIPL	F4 → P4		−0.09 (−0.24–0.05)	0.599	0.228	−0.04 (−0.21–0.13)	0.413	0.651	0.36 (0.20–0.53)	0.532	<0.001	0.31 (0.13–0.48)	0.425	<0.001	0.37 (0.17–0.57)	0.388	<0.001	0.30 (0.08–0.52)	0.232	0.008

List of Regions of Interest (ROIs) and directions of electrode pairs (source → receiver) revealed by conjunction analysis of written and pictorial joke processing. Statistics for complete humour processing contrast presented as within-group and within-modality mean DTF beta values with confidence intervals in appropriate epochs as well as between-group differences (i.e. interaction with group) effects. ROIs definition: L, left; R, right; ventromedial prefrontal cortex (vmPFC, BA 10); dorsomedial prefrontal cortex (dmPFC BA 8/32); dorsolateral prefrontal cortex (dlPFC, BA 9); inferior frontal gyrus (IFG, BA 44/45); anterior temporal lobe (aTL, BA 21/22); posterior temporal lobe (pTL, BA 37); temporoparietal junction (TPJ, BA 40); inferior parietal lobule (IPL, BA 39); precuneus (Prec, BA 7/31).

3. Results

3.1. Behavioural data

Between-group comparisons of the means of comprehensibility and funniness ratings revealed several significant differences. First, for the funny punchlines we found that the clinical subjects revealed a lower level of understanding of written and pictorial jokes. Second, absurd punchlines were assessed as more understandable by the schizophrenia group as compared to controls for written and pictorial jokes. Third, the funniness of absurd punchlines was rated higher by subjects with schizophrenia for both written and pictorial jokes. Fourth, the funniness of neutral punchlines was rated higher by the schizophrenia group for cartoons. Lastly, reaction times were significantly higher in the clinical group in all but one comparison. Scores and reaction times for ratings of all types of punchlines are presented in Table 2.

3.2. EEG results

The effective connectivity maps of neural activation propagation between examined ROIs during humour processing are presented for three contrasts: incongruity detection (Fig. 1); incongruity resolution and elaboration (Fig. 2) and complete humour processing (Fig. 3). In the present paper we reported detailed DTF statistics only for selected directions revealed by conjunction analysis of between-group differences for written and pictorial jokes, i.e. significant interaction effects with group (Tables 3–5). The complete lists of significant ROIs with directions of electrode pairs in 5 epochs containing the detail within-group and within-modality DTF statistics as well as mixed linear model interaction effects for between-group differences are reported for three assessed contrasts in Tables 3–5 and Supplementary Figs. 1–3.

4. Discussion

To the best of our knowledge, the present paper for the first time investigates the dynamics of cortical propagation of information in the humour-related circuit to identify the neural substrate of humour impairment in schizophrenia. Our results revealed that in schizophrenia, humour processing is related to the temporal differences in figurative language processing and engages an alternate neural circuit which manifests as pronounced abnormal lateralization consisting of diminished activity of the right hemisphere together with greater activation in the left hemisphere, as compared to the healthy controls.

The most visible differences in the connectivity pattern have been observed at the early stages (0–2 s) of both absurd (ABS > NEU) and humour (FUN > ABS) processing, which seems to be related to incongruity detection and incongruity resolution impairments in schizophrenia, respectively. Moreover, we found more pronounced effects of absurd processing (ABS > NEU) in healthy controls (0–5 s). On the other hand, network 'silence' was observed at later stages in schizophrenia (3–5 s) (Fig. 1). Thus, it can be assumed that absurd content is more effectively processed in healthy controls than in schizophrenia. Complementary, during incongruity resolution and elaboration (FUN>ABS), the differences were most visible during later stages of humour processing (2–4 s) and manifested themselves as a delayed increased connectivity in schizophrenia (Fig. 2). This phenomenon may be considered as 'belated ignition' of humour resolution in the clinical group. Indeed, the observed temporal alterations in humour processing may also be considered as neural substrate of the behavioural expression of this deficit as well as a nonspecific increase of reaction times.

Moreover, we found distinct directional source/receiver patterns together with reversed lateralization of humour processing in schizophrenia. Firstly, at the early stage (0–1 s) decreased communication was revealed from the right vmPFC to the left dlPFC (incongruity detection) and from the left vmPFC to the right dlPFC receiver (incongruity resolution and elaboration). This functional alteration of the vmPFC in schizophrenia seems to be complementary with our recent fMRI findings pointing at its involvement during incongruity detection (Adamczyk et al., 2017, 2018). Namely, vmPFC seems to play a distinct role in the discrimination of nonsensical content from literal and/or figurative language in healthy controls (i.e. activation/deactivation pattern), but not in schizophrenia.

Considering the important role of the right dlPFC in incongruity detection and resolution, it should be noted that in healthy controls absurd content was processed more extensively by the right hemisphere receivers in fronto-parietal regions. In contrast, in schizophrenia absurd processing is related to the increased propagation to the left IPL. Specifically, during incongruity resolution in healthy controls, the right IPL and bilateral TPJ serve as information sources only, whereas, in schizophrenia the left IPL serves either as a receiver during incongruity detection and as a source during its resolution. This indicates important differences within both TPJs as their activity is much less pronounced in schizophrenia. All the above may reflect the impaired process of obtaining coherence in semantic meaning. Yet, the relative 'silence' of fronto-temporo-parietal connections within the right hemisphere may reflect the hypofunction of the pTL/IPL during incongruity detection observed in our earlier investigation (Adamczyk et al., 2017, 2018).

The dominance of the left hemispheric communication in schizophrenia indicates a reversed pattern of lateralization and suggests the existence of alternative pathways of humour processing in schizophrenia, i.e. critical engagement of the left IPL and precuneus (Fig. 3). This additional engagement of the precuneus needs to be emphasized as the most pronounced example of the alternative pathway. Notably, as a result of lateralization differences, the weaker right hemisphere connectivity activity may explain the weaker BOLD signal found in schizophrenia subjects during processing of the jokes (Adamczyk et al., 2017, 2018).

At last, we show network disturbances in individuals with schizophrenia that accompany weakened and/or abnormal discrimination between the three assessed conditions (FUN, NEU, ABS) (Tables 3–5 and Supplementary Figs. 1–3). This may reflect an altered process of obtaining semantic coherence or detecting nonsense which manifests clearly at the behavioural level. Generally, our results are in line with findings on abnormal language processing in schizophrenia (e.g. the N400 effect; Iakimova et al., 2005; Schneider et al., 2015). The specific between-group differences were observed across all stages of humour processing. This suggests that in schizophrenia, individuals have impaired ability to discriminate between the three types of punchlines (impaired incongruity detection process) that occurs early during joke processing and uses alternative pathways at later stages (incongruity resolution and elaboration). This possibly forms a general compensatory mechanism, responsible for altered behavioural expression. One of the most vivid examples of these differences is that during incongruity detection the highest information flow rate observed in healthy controls was frequently accompanied by its opposite or undifferentiated pattern in clinical subjects (i.e. lowest flow rate for the absurd condition or weakened dissociation between conditions; Supplementary Fig. 1). Similarly, during incongruity resolution and elaboration the highest connectivity rate in healthy controls was frequently observed for funny content, while in the schizophrenia group the funny condition was often associated with the lowest flows (Supplementary Fig. 2–3). At the same time, clinical subjects revealed the strongest connectivity for absurd and/or neutral content in these connections. Finally, it may be concluded that the primary source of the impaired humour processing in schizophrenia is related to the incongruity detection process which manifests as weakened ability to discriminate nonsensical and funny content.

The presented DTF results support recent neuroimaging studies that indicate abnormalities of brain morphology and its functional connectivity in schizophrenia (Asami et al., 2013; Cui et al., 2017; van den Heuvel et al., 2010; Makris et al., 2017; Zhang et al., 2017), which is

reciprocally related to diverse lateralization within the language processing network (Leroux et al., 2013, 2014, 2015; Matsumoto et al., 2001; Sheng et al., 2013; Son et al., 2017) and which may be considered in terms of compensatory recruitment of optional neural circuits (Cobia et al., 2012; Mashal et al., 2014; Morgan et al., 2010; Murray et al., 2010; Tan et al., 2006) as characteristic of this illness. Our results are complementary with other neuroimaging studies which found that fronto-temporo-parietal connections are essential for language, attention, and an integrative higher level of visual and auditory processing (Burks et al., 2017; Makris et al., 2013; Ptak et al., 2016) as well as that of individuals with schizophrenia which revealed the abnormalities in fronto-temporal (van den Heuvel et al., 2010), fronto-parietal (Nielsen et al., 2017) and/or temporo-parietal connectivity (Asami et al., 2013; Zhang et al., 2017, 2018). Overall, all these findings strongly agree with our effective connectivity results on the abnormal information flow in language- and humour-related networks, which may be presumed to be a core feature of incongruity detection as well as resolution and elaboration impairments in schizophrenia.

Although the present study reveal pioneering results on differences in effective connectivity during humour processing in schizophrenia outpatients and healthy controls, some limitations of our study need to be discussed before final conclusion. First of all, despite commonly used in research and experimental design, the theory and model of the three-step humour processing (Suls, 1972; Wyer and Collins, 1992; Chan et al., 2013) provides some methodological problems and is still highly hypothetical and speculative, especially when considering the complex nature of humour phenomenon (Veatch, 1998). Yet, our results focus only on the cognitive (i.e. logical) aspects of humour processing (i.e. comprehension of intended-to-be-funny written jokes/cartoons) omitting the emotional and social aspects of this process. Next, regarding the nonspecificity of our results, as we found reversed pattern of lateralization during humour processing, this effective connectivity patterns may be easily expanded on other higher order cognitive functions in schizophrenia. Importantly, as the studied processes of humour are a significant extent based on nonspecific cognitive processes, they can be considered an example of broader cognitive dysfunctions in schizophrenia. Finally, the presented results of effective connectivity methods applied in punchline-based humour comprehension task, may serve broadly as exact example of connectivity methods, which allowed to give an insight in patterns of propagation of information flow with relatively good time resolution during higher order cognitive processing in schizophrenia.

In conclusion, our effective connectivity results revealed that impaired humour processing in schizophrenia is akin to the altered discrimination between literal, figurative and nonsensical sentences, involving lesser engagement and/or network deactivation in the right hemisphere along with abnormal leftward shifted lateralization patterns during processing of funny content. Moreover, present findings indicate that compensation of this deficit may be related to the recruitment of alternative neural network processing in the left hemisphere.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.schres.2019.05.008.

Contributors

Dr. Adamczyk was involved in literature review, study design and execution, i.e. collection of the neuropsychological assessments, EEG recordings, interpretation of the data, writing of the first draft and co-writing of the manuscript. Dr. Wyczesany was involved in experimental procedure design and programming, data analysis and interpretation and co-writing of the manuscript. MSc Daren was involved in execution of this study, collection of the neuropsychological assessments, EEG recordings, behavioural data analysis and co-writing of the manuscript. All authors contributed to and have approved the final version of the manuscript.

Role of the funding source

This study was supported by the National Science Centre, Poland (grant no 2014/13/B/HS6/03091).

Declaration of Competing Interest

All authors declare no conflicts of interest.

Acknowledgments

We are cordially grateful to all participants for their involvement in this study, as well as to the staff of occupational therapy workshops and rehabilitation centres in Krakow for their assistance in carrying out this work. We are heartily thankful to Joanna Wieczorek for her work on data analysis, to Dr. Piotr Błądziński for conducting psychiatric assessments (PANSS), verifying schizophrenia diagnosis (ICD-10), and collecting information about medication treatment in the clinical group and to Dr. Andrzej Cechnicki for his great help in carrying out this work. Finally, we are thankful to Mike Timberlake for proofreading of the manuscript.

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