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EEG correlates of spontaneous self-referential thoughts: A cross-cultural study

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ABSTRACT

The default mode network (DMN) has been mostly investigated using positron emission tomography and functional magnetic resonance imaging (fMRI) and has received mixed support in electroencephalographic (EEG) studies. In this study, after sLORETA transformation of EEG data, we applied group spatial independent component analysis which is routinely used in fMRI research. In three large and diverse samples coming from two different cultures (Russian and Taiwanese), spontaneous EEG data and retrospective questionnaire measures of subject's state, thoughts, and feelings during the EEG registration were collected. Regression analyses showed that appearance of spontaneous self-referential thoughts was best predicted by enhanced alpha activity within the DMN. Diminished theta and delta activity in the superior frontal gyrus and enhanced beta activity in the postcentral gyrus added to the prediction. The enhanced alpha activity prevailed in the posterior DMN hub in Russian, but in the anterior DMN hub in Taiwanese participants. Possible cross-cultural differences in personality and attitudes underlying this difference are discussed.

1. Introduction

Till recently, the investigation of spontaneous mental processes was beyond the scope of most neuroimaging studies. The situation has changed drastically during the last decade. This became possible owing to two parallel developments. Firstly, fMRI and PET studies of synchronized spontaneous low-frequency oscillations between the brain's areas have revealed a number of so-called resting state networks (RSNs) (Biswal et al., 1995; Lowe et al., 1998) whose possible role in spontaneous mental processes is hotly debated. Second development started after the discovery of the so-called default-mode network (DMN). The DMN concept comes from an emergent body of evidence showing a consistent pattern of deactivation across a network of brain regions that occurs during the initiation of task-related activity (Raichle et al., 2001; Raichle and Snyder, 2007). The DMN includes the precuneus/posterior cingulate cortex (PCC), the medial prefrontal cortex (MPFC), and medial, lateral, and inferior parietal cortex (although some other brain regions, e.g., the medial temporal lobe, are also frequently included in the DMN). Although deactivated during task performance, this network is active in the resting brain. A notable exception to this general pattern occurs in relation to tasks requiring self-referential thought and social cognition (Buckner et al., 2008; Mitchell, 2006; Raichle et al., 2001). Correspondingly, many authors suggested that the DMN is somehow involved in self-referential processes and social cognition (Boly et al., 2008; Christoff et al., 2003; David et al., 2007; Golland et al., 2007; Gusnard et al., 2001; Mitchell, 2006; Wicker et al., 2003). The study of task-related activation/deactivation and studies of synchronized spontaneous low-frequency oscillations have converged in admitting the DMN as one of RSNs (Raichle et al., 2001).

The quest to fully elucidate the function of DMN and other RSNs requires a solid understanding of the link between neuroimaging findings and their electrophysiological underpinnings. Electroencephalogram (EEG) and fMRI represent different aspects of brain activity. Their relationship can thus yield insights not available from one modality alone. If DMN is involved in self-referential processes, as existing fMRI evidence appears to suggest, the study of EEG correlates of these processes may bring important information on how the same psychological processes are reflected in the EEG and fMRI domains. There could be different approaches to the study of fMRI and EEG manifestations of such phenomenon as DMN. Firstly, because simultaneous registration of both signals is now available, raw fMRI and EEG measures could be correlated with each other. Secondly, instead of raw fMRI and EEG measures, patterns of temporally or spatially synchronized networks could be revealed in one or both domains and the correlations could be calculated between these patterns. Lastly, measures of DMN-related behavioral or psychological processes could be used as the criterion variable that could be correlated with respective fMRI or EEG measures (Laufs, 2008).

Many simultaneous EEG–fMRI studies have noted correlations between the DMN blood-oxygen-level-dependent (BOLD) signal and EEG gamma (Mantini et al., 2007), beta (Laufs et al., 2003b; Mantini et al., 2007), alpha (Laufs et al., 2003a; Mantini et al., 2007), and theta (Meltzer et al., 2007; Scheeringa et al., 2008) oscillations.

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Most of the studies have found mainly negative correlations between EEG spectral power (particularly in alpha band of frequencies) and BOLD signal in cortical areas (see e.g., Laufs, 2008 for a review). Laufs (2008) notes that the failure across studies to identify an average cortical BOLD signal pattern which is positively correlated with alpha power may be explained by nonuniform brain activity at the population level during periods of prominent alpha oscillations which fMRI group analysis must fail to detect (Laufs et al., 2006).

In the study by de Munck et al. (2007, 2008), time variations of the occipital alpha band amplitudes were correlated to the fMRI signal variations to obtain insight into the hemodynamic correlates of the EEG alpha activity. It was found that: (1) the alpha band response function of the thalamus is mainly positive. (2) The response functions at the occipital and left and right parietal points are similar in amplitude and timing. (3) The peak time of the thalamus is a few seconds earlier than that of occipital and parietal cortex. A general negative correlation was found between heart beat intervals and alpha power, but inclusion of this confounder had a negligible effect to alpha-BOLD correlations. Wu et al. (2010) found widespread alpha hemodynamic responses and high functional connectivity during eyes-closed rest, while eyes open resting abolished many of the hemodynamic responses and markedly decreased functional connectivity.

Jann et al. (2010) note that when investigating BOLD correlates of EEG rhythms, these correlates resembled the RSNs, suggesting that the different RSNs assemble through synchronization of electric activity as measured by EEG. Namely, BOLD correlates of electrical activity in the alpha (8–12 Hz) and beta (17–23 Hz) frequency bands displayed striking similarity with the DMN as it was described in other publications, suggesting that the RSNs may be organized by neuronal activity at specific frequencies. Martinez-Montes et al. (2004) demonstrated a method correlating EEG 'atoms' with fMRI 'atoms' and identified the alpha-band atom to include parieto-occipital cortex, thalamus, and insula. Mantini et al. (2007) incorporated into their analysis EEG bands between 1 and 50 Hz averaged across the entire scalp and correlated with these bands the fMRI time courses of resting state networks identified by the use of independent component analysis (ICA). RSNs 1 (DMN) and 2 (dorsal attentional network) had stronger relationship with alpha and beta rhythms, albeit in opposite directions, with RSN1 showing positive whereas RSN2 showing negative correlation with alpha and beta rhythms. Jann et al. (2009) show that the BOLD correlates of global EEG synchronization in the alpha frequency band are located in brain areas involved in the DMN. These results confirm the hypothesis that specific RSNs are organized by long-range synchronization at least in the alpha frequency band (Jann et al., 2009). Jann et al. (2010) report on the topographic association of EEG spectral fluctuations and RSN dynamics using EEG covariance mapping. T-mapping of the covariance maps indicated that the strongest effects were again in the alpha and beta bands. DMN activity was found to be associated with increased alpha and beta1 band activity. Sadaghiani et al. (2010) showed that global field power of upper alpha band oscillations is positively correlated with activity in a network overlapping with the DMN and is negatively correlated with activity in the dorsal attention network which is most prominently involved in selective spatial attention. Brookes et al. (2011) analyzed magnetoencephalographic (MEG) data using a unique combination of beamformer spatial filtering and independent component analysis. This method resulted in RSNs with significant similarity in their spatial structure compared with RSNs derived independently using fMRI. In this study, the DMN was identified using MEG data filtered into the alpha band.

In sum, this evidence suggests that alpha and beta oscillations appear to positively correlate with fMRI-DMN and negatively with attentional networks (although, correlations with other frequency bands have also been noted, e.g., Mantini et al., 2007; Meltzer et al., 2007; Scheeringa et al., 2008). Most of these studies correlated temporal dynamics of averaged or 'global' spectral EEG variables with time courses of spatially correlated networks derived from spontaneous fluctuations of fMRI BOLD signal by means of ICA and similar techniques. The reported correlations imply that in resting condition, the spontaneous fluctuations of 'global' EEG alpha and beta activity notably covary with spontaneous fluctuations of DMN's BOLD signal. Whatever important these observations may be, they in themselves do not speak anything about behavioral or psychological processes underlying this covariance. As Laufs (2008) noted, of the neural processes reflected in both EEG and fMRI there may be measurable behavioral manifestations. It could be argued that from both theoretical and practical point of view these behavioral manifestations are most important.

Unfortunately, studies investigating EEG correlates of self-referential processes are very scarce and few of them did it in resting condition and analyzed spectral EEG information. Mu and Han (2010) used wavelet analysis to calculate non-phase-locked time-frequency power associated with encoding of trait adjectives referenced to the self or the familiar other. Relative to other-referential traits, self-referential traits induced event-related synchronization of theta-band activity over the frontal area and of alpha-band activity over the central area. In contrast, event-related desynchronization associated with self-referential traits was observed in beta-band activity over the central–parietal area and in gamma-band activity over the fronto-central area. eLORETA analysis during eyes-closed rest and Transcendental Meditation identified sources of alpha activity in midline cortical regions that overlapped with the DMN (Travis et al., 2010). Congedo et al. (2010) used group ICA of rest EEG data on large sample of subjects and found several components whose topography overlapped with DMN. Two components which were characterized by clear peak in alpha frequencies had maximal activity in posterior cortical regions including the cuneus/precuneus and PCC. The authors suggest that these components may represent activity involved in self-centered mental imagery, during both personal past and personal future thinking.

It should be noted that differences in EEG and fMRI results could be partly explained by different analysis approaches that are traditionally used in the two domains. Thus, blind source separation techniques are increasingly becoming popular both in EEG and in fMRI research, but there are several principal differences in how these techniques are applied in the two domains. In EEG research, temporal ICA (TICA) is usually used, whereas in fMRI research, spatial ICA (SICA) is almost exclusively applied. There are several reasons for this, of which the most important is that the spatial dimension is much larger than the temporal dimension in fMRI, whereas for EEG, the temporal dimension is much larger than the number of sources (Calhoun et al., 2001a). SICA and TICA yield similar results if there is one predictable task-related component or two components that are uncorrelated in both space and time. However, SICA and TICA diverge if the predictable components are highly correlated in space or time, respectively (Peterson et al., 2000). Another difference is that in EEG research, ICA is usually applied to each subject's data separately. Obtained independent components (ICs) are said to represent temporally independent signal sources and have scalp maps that nearly perfectly match the projection of a single equivalent brain dipole (Delorme and Makeig, 2004). Thus, such approach is perfectly suited for studying temporally uncorrelated spatially local processes that could be modeled by a single equivalent brain dipole, but it is less suitable for studying more spatially extended or temporally correlated processes. Besides, following such ICA, there is no natural and easy way to identify a component from one subject with a component from another subject (Makeig et al., 2004). A strategy that is most frequently used is to combine individual ICs across subjects with clustering techniques (Esposito et al., 2005; Onton et al., 2006). In fMRI research, another approach, which is called group ICA, is mostly used. Aggregate data containing observations from all subjects are created, then, a single set of ICs is estimated and back-reconstructed in the individual data (Calhoun et al., 2001b; Schmithorst and Holland, 2004). Knyazev et al. (2011) used group SICA of sLORETA-transformed EEG data in rest and during two experimental tasks and found that alpha band spatial patterns simultaneously showed a considerable overlap with the DMN and high correlations with presumptive DMN function-related outcomes. It should be borne in mind however that comparative to fMRI, this method has much lower spatial resolution which stems from the low spatial resolution of the EEG source imaging techniques. That means that localization of underlying processes might be erroneous if there are several closely spaced sources that correlate with each other in space and/or time. Using MEG instead of EEG may partly overcome this limitation. An excellent example of this gives the study by Brookes et al. (2011) who applied to MEG data a combination of beamformer spatial filtering and independent component analysis and demonstrated the potential of MEG as a tool for understanding the mechanisms that underlie RSNs and the nature of connectivity that binds network nodes.

In this study, we aimed to replicate the findings of the Knyazev et al.'s (2011) study using larger datasets and denser electrode arrays. Secondly, we aimed to compare observed effects in subjects of different cultures (Russian and Taiwanese). Because the self of each individual develops in a specific socio-cultural context, it may undergo strong modulations and form a particular style in order to efficiently interact with other individuals in social environments (Han and Northoff, 2009). Social and cultural psychologists have shown ample evidence for cultural difference in the self and self-related processing (Markus and Kitayama, 1991; Zhu and Han, 2008). Unlike the Western philosophy that emphasizes the unique dispositions to define the self, East Asian philosophy puts strong emphasis on human connections with each other in social contexts (Zhu and Han, 2008). Existing data show that these cultural differences extend to the neural substrates underlying the processing of self-related information. Thus, a direct comparison of English-speaking Westerners and monolingual Chinese subjects in an fMRI study shows that Chinese individuals use the same brain structure (namely, the medial prefrontal cortex, MPFC) to represent both the self and a close other, whereas Western subjects use it to represent exclusively the self (Zhu et al., 2007). Although Russia is not a typical European country and Russian culture consists of a mixture of Western and Eastern values, in terms of individualism–collectivism dimension it seems to be closer to Western than to Eastern cultures (Suh et al., 1998). We have not been able to find any study of cross-cultural differences in EEG correlates of self-referential processes. We also were not able to find any study that would compare self-referential processes in Russians in comparison with a typical Western or a typical Eastern population. Therefore, this study could be considered as a first attempt to fill this gap.

2. Methods

2.1. Subjects

Resting EEG data were collected in three samples. First Russian sample included 60 participants (32 men and 28 women; age range 17 to 30 years, mean = 20.4, SD = 2.5). A part of this sample (48 participants) was used in the Knyazev et al.'s (2011) study. Second Russian sample included 58 participants (37 men and 21 women; age range 19 to 77 years, mean = 41.2, SD = 20.8). Taiwanese sample included 42 participants (26 men and 16 women; age range 18 to 33 years, mean = 27.1, SD = 3.3). All samples consisted of healthy volunteers. The first Russian sample and the Taiwanese sample mostly included university students, whereas the second Russian sample included participants of different occupations. All applicable subject protection guidelines and regulations were followed in the conduct of the research in accordance with the Declaration of Helsinki. All participants gave informed consent to the study. The study has been approved by the Institute of Physiology, Russia, and the Institute of Statistical Science, Academia Sinica, Taiwan ethical committees.

2.2. Instruments and procedures

Experimental study of internal mental life using introspective methods was started in the late 19th century by Wilhelm Wundt and was continued in 20th century in works by Singer, Antrobus, and others (see Buckner et al., 2008 for review). In the past decade, the study of spontaneous cognition has introduced novel experimental approaches to explore the content of people's internal mental states, such as thought sampling or experience sampling (see Smallwood and Schooler, 2006 for review). A limitation of these latter approaches is that they interfere with the spontaneous thought, most typically to terminate its occurrence (Giambra, 1995). This is a reason as to why retrospective methods of thought sampling, such as questionnaire measures, are still widely used (Smallwood et al., 2004). It has been argued that retrospective measures confound mind-wandering with awareness/memory of mind wandering because they depend on an individual's ability to monitor attention (Schooler et al., 2005). Generally, however, these two approaches (i.e., thought sampling and retrospective measures) are reliably correlated (Smallwood and Schooler, 2006). In this study, we used a brief (35 items) retrospective Spontaneous Thoughts Questionnaire (STQ) which was designed to measure different aspects of subject's state, thoughts, and feelings during spontaneous EEG registration. All items were measured on a five-point Likert scale. The questionnaire was initially created in Russian by the first author and was subsequently translated into Chinese by a Taiwanese bilingual language expert. The face validity of the Chinese translation was examined and modified by a senior psychometrician who also interviewed a few volunteer subjects on the wordings of items in the questionnaire. The final Chinese STQ version had minor corrections based on the interview results. Additionally, selected items were translated into English by the fourth author and sent to the first author for evaluation. Factor analysis of all questionnaire items (principal components factor analysis with varimax rotation) was conducted in the total sample of subjects (N = 160). Examination of the eigenvalues and scree plot for a principal component analysis revealed that a four-factor solution best fitted the data. Accordingly, four scales were created that described nervousness/negative emotion/lack of positive emotion (NE, example items: “felt nervous”, “experienced negative emotions”, “was calm and relaxed” — reverse scoring, “liked the procedure” — reverse scoring, Cronbach's alpha = 0.84); self-referential thought (SRT, example items: “thought about something pleasant that is going to happen to me in the near future”, “recollected episodes from my own life”, “most of the time, thoughts of my recent past recurred to me”, “most of the time, I was absorbed in my private thoughts”, Cronbach's alpha = 0.69); arousal level (example items: “was almost asleep” — reverse scoring, “was quiet and relaxed” — reverse scoring, “was somewhat heated”, “was very excited”, Cronbach's alpha = 0.72); attention to environment (ATT, “my attention was mostly directed to external stimuli”, “most of the time, I listened to sounds and skin sensations”, “did not pay any attention to external stimuli” — reverse scoring, Cronbach's alpha = 0.65). The SRT scale (SRTS) was used to measure individual differences in mental processes presumably related to DMN's activity.

Participants were seated in a soundproof dimly illuminated room and did not receive any instruction. According to Gale (1983), experimental conditions consisting of rest with repeated opening and closing of the eyes are rated ‘moderately arousing’ and therefore optimum for the study of EEG correlates of mental processes that are inherent to the subject. Our procedure consisted of 6 one-minute recordings (3 with eyes closed and 3 with eyes open) alternating pseudo-randomly. Only the eyes closed condition was analyzed in this study because previous research has shown that self-referential thoughts correlate with EEG spectral power in the eyes closed, but not in the eyes open condition (Knyazev et al., 2011). Participants were asked to fill out the STQ questionnaire just after the spontaneous EEG registration.

2.3. EEG recording

The sample 1 EEG data were recorded in Novosibirsk, Russia, using 32 silver–silver chloride electrodes mounted in an elastic cap on the positions of the international 10–20 system. The signals were amplified with a multichannel biosignal amplifier with a gain of 250 and a bandpass 0.05–70 Hz, −6 dB/octave and continuously digitized at 300 Hz. The sample 2 (Novosibirsk, Russia) EEG data were recorded using 64 silver–silver chloride electrodes positioned according to a modified version of the international 10/20 System (American Electroencephalographic Society, 1991). The EEG was digitized at a rate of 1000 Hz and amplified using "Neuroscan (USA)" amplifiers with a gain of 250 and a bandpass of 0 to 70 Hz. The sample 3 EEG data were recorded in Taiwan using 132 channels. The EEG electrodes were placed on 128 head sites according to the extended International 10–10 system. The Quik-Cap128 NSL was used for electrode fixation. The signals were amplified using "Neuroscan (USA)" amplifiers, with 0.1–100 Hz analog bandpass followed by a 50-Hz notch filter and continuously digitized at 1000 Hz. The actual positions of each electrode and the three fiduciary points (nasion and preauricular points) were recorded by means of a digitizer (Polhemus).

To compare the skull shape in Taiwanese and Russian participants, we used data from our recent experiment in which the actual positions of each electrode were recorded in a Russian sample which closely matched the sample 1 from the current study in terms of ethnicity, age, and gender (35 subjects, 17 females, age range 17 to 30 years, mean = 20.2, SD = 5.5). The cephalic index was calculated as 100 × head breadth/head length. The head breadth was the distance from the left preauricular point to the right preauricular point and the head length was the distance from nasion to Oz. In Russians, the cephalic index (SD) was 86 (2.8). In Taiwanese, it was 84.5 (3.9). The difference was not significant (T = 1.66, p = .101).

All recordings were performed using a fronto-central electrode as ground, and electronically linked mastoid electrodes as reference. The horizontal and vertical electrooculogram (EOG) was registered simultaneously. Electrode impedances were at or below 5 kΩ for all electrodes used in the analysis. EEG data were artifact-corrected using ICA via EEGLAB toolbox (http://www.sccn.ucsd.edu/eeglab/) retaining minimally 20 out of 30 (for the first sample), 40 out of 60 (for the second sample), and 100 out of 128 (for the third sample) components and recomputed to average reference.

2.4. 3D source reconstruction

To determine the cortical sources of EEG activity, sLORETA (Pascual-Marqui, 2002) was applied to the data. The sLORETA is a linearly distributed solution that is based on standardized values of the current density estimates given by the minimum norm solution. The sLORETA functions on the assumption that the EEGs measured on the scalp are generated by highly synchronized post-synaptic potentials occurring in large clusters of neurons (Pascual-Marqui, 2002). The sLORETA uses a three-shell spherical head model registered to the digitized Talairach and Tournoux (1988) atlas (Brain Imaging Centre, Montreal Neurological Institute). The solution space is restricted to cortical gray matter and parahippocampal areas. The sLORETA yields images of standardized current source density of a total of 6430 voxels at 5-mm spatial resolution. Artifact-free epochs of 1.7 s duration were supplied for cross-spectrum calculation in sLORETA. The number of epochs varied in different subjects from 85 to 210. Subsequently current source densities of delta (2–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (30–45 Hz) oscillations were estimated in sLORETA. The regularization factor was set at 1/100 (Congedo, 2006).

2.5. Independent component analysis

In this study, we used the group SICA, because it directly estimates components that are consistently expressed in the population, involves the least amount of user interaction and is straightforward to compare with the existing framework for group ICA of fMRI data (Calhoun et al., 2001b). First, current source density estimates for the five EEG frequency bands were calculated using sLORETA. Second, group SICA was applied to sLORETA images in a fashion that is routinely used in fMRI research (Knyazev et al., 2011, 2012). SICA was performed using the Group spatial ICA for fMRI Toolbox (GIFT, Version 1.3i; http://icatb.sourceforge.net/), using methods and algorithms described in Calhoun et al. (2001b, 2004). The number of extracted components was initially estimated from the data using the minimum description length (MDL) criteria. Basing on these estimates, 20 components were retained for the Study 1 data and 40 components for the Study 2 and 3 data.

One-sample T-tests in SPM8 were used to assess the statistical significance of each component. Each subject's respective component image (z-score spatial map) was entered into a second-level random-effects analysis and assessed statistically using a threshold of $P_{FDR} =$ 0.05 (whole-brain corrected) and minimum cluster size of 8 contiguous voxels. Only the components that were statistically significant across subjects were used in further analyses. In our data, more than 90% of components were statistically significant. All positive voxel values in a respective independent component image (z-score spatial map) were summed for each subject. These values were further used in regression analyses in SPSS, as is described below. This approach to capturing inter-individual differences is based on the following discussion. After initial decomposition on all concatenated datasets at once, the components are back reconstructed in each individual subject. After that, each component is more pronounced in some subjects and may be weak or absent in others. If the component is strongly pronounced in a particular subject, brain areas in which this component has maximal activity will, in this subject, have high values. After scaling of spatial maps in z-scores, these areas will have, in this subject, high positive values. In some other subject, where this component is weak, these areas will have small values. Therefore, summing and comparing across subjects the positive values in z-transformed spatial maps of a component allows revealing individual differences in intensity of this component. This method is described in the paper by Allen et al. (2011a).

To reduce observer bias in identifying the independent component patterns with description in fMRI literature networks, we performed a spatial sorting analysis in GIFT. For each respective set of Group ICA results, independent components were spatially correlated with an anatomically defined template and were ranked according to a 'highest correlation' criterion (Pearson's r) with this anatomy (for a similar approach see Garrity et al., 2007; Greicius et al., 2004; Harrison et al., 2008). In this study, we used several templates that were generated using the Wake Forest Pick atlas toolbox. The anterior DMN hub (ADMN) template included the superior frontal gyrus (BAs 8/9/10) and the anterior cingulate cortex (BAs 11/32). The posterior DMN hub (PDMN) template included the posterior parietal cortex (Brodmann's area 7), the occipitoparietal junction (Brodmann's area 39), the posterior cingulate, and the precuneus. Both bilateral and unilateral (left and right) templates of these areas were created. The similarity indices with each template were computed based on positive (after Z-transformation) loads (Calhoun et al., 2001a).

2.6. Statistical analysis

Associations between IC scores and SRTS scores were analyzed using stepwise multiple regression method in SPSS. Scores of all statistically significant components in all frequency bands were simultaneously entered in a regression equation as independent variables to predict SRTS scores. There are potential pitfalls in regression models with so many independent variables. The first one is the multiple comparison issue. Bonferroni correction was applied to correct for multiple comparisons and to reveal statistically significant predictors. Another problem is the problem of multicollinearity. Multicollinearity develops when one or more of the independent variables are highly correlated with one or more of the other independent variables. If the independent variables are not perfectly correlated, but only highly correlated, there exists a solution for the regression coefficients but the estimates, while unbiased, are unstable, and their standard errors are typically large (Gordon, 1968). We used the variance inflation factor (VIF) as a measure of the collinearity (see e.g., O'Brien, 2007 for mathematical definition of this measure). It is frequently suggested that a VIF of less than 10 is indicative of inconsequential collinearity (Hair et al., 1995; Marquardt, 1970; Menard, 1995). However, O'Brien (2007) states that in some cases values of the VIF of 10, 20, 40, or even higher do not, by themselves, discount the results of regression analyses.

3. Results

3.1. Psychometric results

In the total sample of subjects (N = 160), age correlated negatively with NE (r = −.16, p = .036) and ATT (r = −.26, p = .001). There were no gender differences on any of the four psychometric variables. The two Russian samples did not differ from each other on psychometric variables, but there were significant differences between Russian and Taiwanese participants. Specifically, Taiwanese participants scored higher than Russian participants on NE (T = 6.53, p < .001) and ATT (T = 4.03, p < .001) scales. The difference remained significant when only younger Russian participants (i.e., < 40 years) were retained in the analysis (T = 5.43, p < .001 and T = 3.20, p = .002 for NE and ATT, respectively).

3.2. Study 1

Multiple regression analysis (98 independent predictors after exclusion of no significant components) revealed that SRTS scores were best predicted by an alpha band component (β = .48, p < .0005, R square = .16, VIF = 1.4) that showed maximal activity in the precuneus (BA 19, MNI coordinates: x = 35, y = −85, z = 35) and the largest spatial correlation with the PDMN template (r = .53). Fig. 1 shows anatomy of this component.

Other predictors were not significant after Bonferroni correction.

3.3. Study 2

Stepwise multiple regression analysis (195 independent predictors after exclusion of no significant components) revealed two significant predictors of SRTS scores. An alpha band component that showed maximal activity in the precuneus (BA 19, MNI coordinates: x = −40, y = −75, z = 40) and the second largest spatial correlation with the left PDMN (r = .35) appeared at the top of the list (β = .58, p < .0001, R square = .24, VIF = 1.28). Fig. 2 shows anatomy of this alpha component.

The alpha component, which showed the largest spatial correlation with the left DMN (r = .42), was not retained in model during the stepwise regression analysis, but bivariate correlation analysis (Pearson) revealed that it showed the second strongest correlation with SRTS scores (r = .48).

Theta component, which showed maximal activity in the superior frontal gyrus (BA 6, MNI coordinates: x = 10, y = 20, z = 65) and a considerable spatial overlap with the anterior DMN (the third largest spatial correlation with the ADMN template, r = .18), was the second strongest predictor of SRTS scores (β = −.50, p < .0001, R square = .15, VIF = 1.54) (Fig. 3).

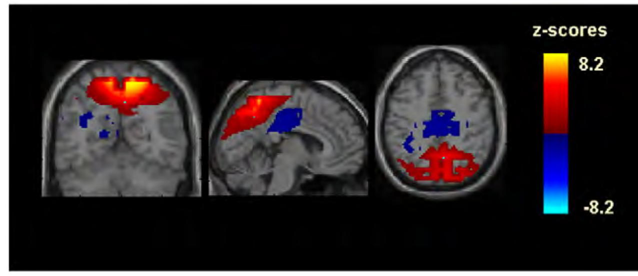

Fig. 1. Study 1. Anatomy of the alpha component that showed the strongest (positive) association with SRTS scores and the largest spatial correlation with the PDMN template. Spatial maps are scaled in z-scores.

Note that the alpha component shows positive, whereas the theta component shows negative correlation with SRTS scores.

3.4. Study 3

Stepwise multiple regression analysis (198 independent predictors after exclusion of no significant components) revealed three significant predictors of SRTS scores. An alpha band component that showed maximal activity in the superior frontal gyrus (BA 6, MNI coordinates: x = 10, y = 20, z = 65) and the strongest spatial correlation with the ADMN template (r = .25) appeared at the top of the list (β = .70, p < .0001, R square = .20, VIF = 2.3). Fig. 4 shows anatomy of this alpha component.

A beta component which showed maximal activity in the postcentral gyrus (BA 2, MNI coordinates: x = −30, y = −40, z = 70) was the second strongest predictor (β = .57, p < .0001, R square = .15, VIF = 1.33). A delta component which showed maximal activity in the superior frontal gyrus (BA 8, MNI coordinates: x = 20, y = 35, z = 55) and a considerable spatial overlap with the anterior DMN (the third largest spatial correlation with the ADMN template, r = .20) was the third strongest predictor (β = −.25, p < .00025, R square = .02, VIF = 1.99). Note that the alpha and the beta components show positive, whereas the delta component shows negative correlation with SRTS scores.

3.5. Formal comparison of Taiwanese and Russian samples

To formally compare Taiwanese and Russian samples and to reveal culture-related differences, the two Russian samples were merged together and the effect of culture on the relationship between SRTS scores and anterior vs. posterior DMN alpha activity was assessed using general linear model (GLM) analysis in SPSS. For this analysis, a combined measure of PDMN vs. ADMN alpha activity (hereafter P/ADMN) was created. The alpha band $PDMN_{IC}$ (here and later subscript IC denotes independent component that showed highest spatial correlation with respective template) and $ADMN_{IC}$ scores were converted to z-scores and $ADMN_{IC}$ scores were subtracted from $PDMN_{IC}$ scores. The resulting measure represented a dimension running from low PDMN/high ADMN alpha activity to high

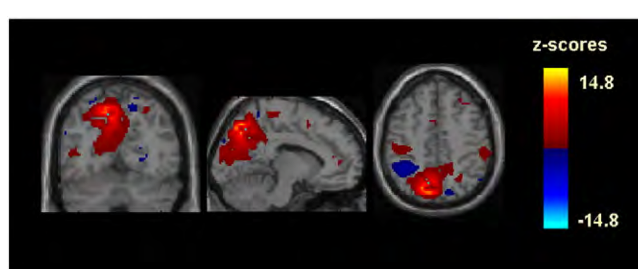

Fig. 2. Study 2. Anatomy of the alpha component that showed the strongest (positive) association with SRTS scores and the second largest spatial correlation with the left PDMN template.

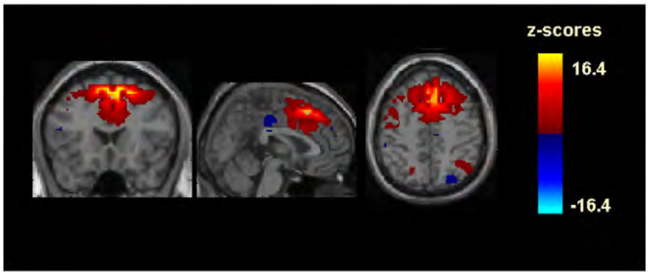

Fig. 3. Study 2. Anatomy of the theta component that showed the second strongest (negative) association with SRTS scores and the third largest spatial correlation with the ADMN template.

PDMN/low ADMN alpha activity. GLM analysis showed a significant culture × P/ADMN interaction, $F(3, 152) = 5.43$, $p = 0.001$, which indicated that in Russian participants, higher SRTS scores are associated with higher alpha activity in the posterior DMN hub, whereas in Taiwanese participants they are associated with higher alpha activity in the anterior DMN hub.

4. Discussion

In this study, multiple regression analysis was used to reveal the strongest predictors of SRTS scores. It should be noted that VIF values for all significant predictors were well below 10, suggesting that collinearity was not an issue in our regression analyses (Hair et al., 1995; Marquardt, 1970; Menard, 1995).

In line with the results that were reported previously (Knyazev et al., 2011), in both Study I and Study II samples, individual differences in the degree of self-reported spontaneous self-referential thought were best predicted by individual differences in the activity of an alpha band component, that considerably spatially overlapped with the DMN's posterior hub. The degree of correspondence between the DMN as determined by neuroimaging and the EEG spatial maps could be quantitatively evaluated by the size of correlations between ICs' spatial maps and spatial templates that were created basing on published neuroimaging data. These correlations are comparable with those reported in relevant fMRI studies using group ICA (see e.g., Harrison et al., 2008). It should be emphasized that the Study II sample was considerably different from the Study I sample both in terms of participant's age and occupation. There were also methodological differences in EEG data acquisition (30 EEG channels in the Study I and 60 EEG channels in the Study II). Taking all this into account, the similarity of results is striking.

Contrary to that, in Taiwanese sample (Study III data), the same mental processes correlated with the activity of an alpha band component, that spatially overlapped with the DMN's anterior hub. It could be concluded that in all samples, EEG correlates of spontaneous self-referential thought are most strongly associated with alpha activity and with the DMN structures, but precise localization within the DMN is different in Russian and Taiwanese samples. Firstly, a possibility that this difference has arisen due to methodological limitations of the current study needs to be ruled out. For example, a systematic bias between Russian and Taiwanese participants due to a difference in skull shape could cause the observed difference. One type of instrument that is used for taking accurate measurements of skull shape, the so-called cephalic index, is attributed to the Swedish anatomist Anders Retzius and measures the breadth and length of the skull. A cephalic index (breadth over length) over 0.8 denotes brachycephaly; one between 0.75 and 0.80 mesocephaly; and one below 0.75 dolichocephaly (Whitaker, 2009). Some researchers have concluded that cephalic index is responsive to environmental changes (Boas, 1912; Gravlee et al., 2003; Kouchi, 2000), while others have found that it is highly heritable and do not respond readily to environmental insults (Sparks and Jantz, 2002). It has been also suggested that in countries with Nordic populations such as Sweden, England, and Germany a large portion of the population was dolichocephalic, whereas in other European and Asian countries most of the population was mesocephalic or brachycephalic (Whitaker, 2009). It is now acknowledged however that individual differences in skull shape within each population are so large that any boundary between groups is arbitrary, just as are the limits defining brachycephaly and dolichocephaly (Whitaker, 2009). We compared the skull shape in Taiwanese and Russian participants and found no significant difference. This is in line with anthropological studies showing that Russian population (particularly in Siberia) is mostly mesocephalic or brachycephalic (Godina et al., 2008; Tschepourkowsky, 1923), as well as East Asian populations (Okazaki, 2010). This allows being reasonably confident that the observed difference in EEG correlates of spontaneous self-referential thought was not due to a systematic difference in skull shape.

To the best of our knowledge, this is the first study that compared EEG correlates of spontaneous self-referential thought in Eastern and Western population (with a reservation that although Russia is not a typical Western country, its culture is closer to Western than to Eastern values), therefore our finding could be considered preliminary and clearly needs replication in the future. In spite of this, existing evidence allows considering possible tentative explanations of the observed difference.

The default network comprises a set of brain regions that are co-activated during passive states and show intrinsic functional correlation with one another. However, there is clear evidence that the brain regions within the DMN contribute specialized functions that are organized into subsystems that converge on hubs (Buckner et al., 2008). Indeed, although SICA of resting state BOLD signal frequently finds a single DMN component (see e.g., Harrison et al., 2008), in higher order models the anterior and the posterior DMN usually branch into different components (see e.g., Allen et al., 2011b; Abou-Elseoud et al., 2010). Maps of the intrinsic correlations within the default network show that it comprises at least two interacting subsystems (Buckner et al., 2008). One subsystem functions to provide information from memory; the second participates to derive self-relevant mental simulations. The medial temporal lobe subsystem provides information from prior experiences in the form of memories and associations that are the building blocks of mental simulation. The medial prefrontal subsystem facilitates the flexible use of this information during the construction of self-relevant mental simulations. These two subsystems converge on the precuneus/posterior cingulate cortex (pC/PCC) (Buckner et al., 2008). Partial correlation network analysis suggests that this latter region may play a pivotal role in the DMN (Fransson and Marrelec, 2008). Indeed, PET studies have shown that the metabolic activity is higher in the pC/PCC than all other regions during rest (Gusnard and Raichle, 2001). It could be suggested that being the place of integration of prior experiences with mental simulations, the pC/PCC sustains a sense of self-consciousness that is engaged in self-referential mental thoughts during rest (for reviews see Cavanna and Trimble, 2006;

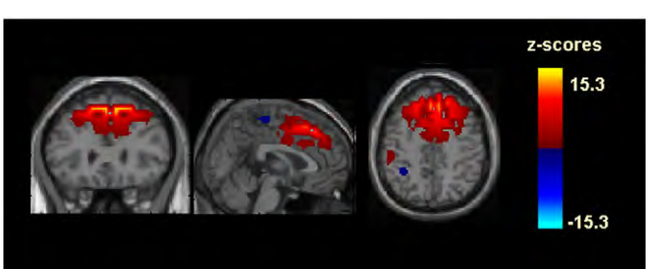

Fig. 4. Study 3. Anatomy of the alpha component that showed the strongest (positive) association with SRTS scores and the largest spatial correlation with the ADMN template.

Buckner and Carroll, 2007) and is commonly associated with positive emotions (Koole et al., 2001).

Converging findings implicate MPFC involvement in both social cognition and self-related processing. The dorsal MPFC have been activated in many studies on the self, which include a strong evaluative or judgmental component (e.g., Johnson et al., 2002; Zysset et al., 2002). More rostral, ventral MPFC regions have been activated in studies that had a self-reflection component (e.g., Kelley et al., 2002; Lieberman et al., 2004; Seger et al., 2004). It appears that social salience which reflects the relation between others and oneself is processed by the MPFC. Thus, MPFC structures have been activated when subjects formed impressions about people as opposed to objects (Mitchell et al., 2005a,b) or observed social interactions between others (Han et al., 2005; Iacoboni et al., 2004). Imaging studies report an overlap between the processing of the self and others in the dorsal and ventral MPFC (Schmitz et al., 2004; Seger et al., 2004). However, neural dissociation between the self and others has been observed within the same regions (Ochsner et al., 2005; Schmitz et al., 2004; Seger et al., 2004). The key issue here is the degree of self-relatedness of the other person; the more the other is identified as self-related, the greater the similarity between MPFC responses to the self and other (Han and Northoff, 2009). Mitchell et al. (2005a,b) found that the more the similar subjects rated others' faces to their own, the greater the activation was observed in the ventral MPFC, suggesting that it is engaged in viewing others in terms of one's own self. Interestingly, a direct comparison of Western and Chinese subjects with regard to self-referential processes found major distinction in the MPFC. Specifically, Chinese individuals appear to use this brain region to represent both the self and a close other, whereas Western subjects use it to represent exclusively the self (Zhu et al., 2007). Moreover, neural activity within the anterior rostral portion of the MPFC during processing of general and contextual self judgments positively predicts how individualistic or collectivistic a person is across cultures (Chiao et al., 2009). MPFC appears to be involved in empathy and altruistic motivation for members of one's own social group. Thus, people generally showed greater response within ACC and bilateral insula when observing the suffering of others, but African-American individuals additionally recruit MPFC when observing the suffering of members of their own social group. Moreover, neural activity within MPFC in response to pain expressed by in-group relative to out-group members predicted greater empathy and altruistic motivation for one's in-group, suggesting that neuro-cognitive processes associated with self identity underlie extraordinary empathy and altruistic motivation for members of one's own social group (Mathur et al., 2010). The common element that activates MPFC appears to be thinking about the complex interactions among people (Buckner et al., 2008).

It could be speculated that spontaneous self-referential thoughts that are not centered on complex social relationships and are commonly associated with positive emotions may be accompanied by enhanced alpha activity in the posterior DMN hub, whereas mental simulations of complex social relationships may engage the MPFC to a greater extent. These mental simulations are frequently associated with negative emotions. It could be further suggested that the former processes may prevail in more individualistic individuals and the latter in more collectivistic ones. In terms of Hofstede's (2001) dimensions of culture, Taiwan is a typical collectivistic culture, whereas Russia appears to be moderate in individualism.

Our data show that Taiwanese participants score much higher on Negative Emotion and externally-oriented attention than Russian participants. That means that they appear to be more nervous and vigilant in the condition of spontaneous EEG registration. This is in line with many cross-cultural studies showing that Eastern populations in general and Chinese and Taiwanese populations in particular are higher on Neuroticism and lower on Extraversion than most Western populations including Russia (see e.g., Allik and McCrae, 2004). Germane to this interpretation, recent studies show that in resting condition, the trait of agentic extraversion that is characterized by habitual positive affect (e.g. Diener et al., 2003) is associated with an increase of spectral power in several frequency bands including alpha in posterior cortical regions that overlap with the DMN's posterior hub and a decrease of spectral power in anterior regions that partly overlap with the DMN's anterior hub (Hewig et al., 2004, 2006; Knyazev, 2009, 2010; Knyazev et al., 2012; Wacker et al., 2006, 2010). Interestingly, it has been shown that mean extraversion scores from 33 countries around the world were substantially positively correlated with individualism (Hofstede and McCrae, 2004).

Summing up, we suggest that in more extraverted, emotionally stable, and individualistic individuals, spontaneous self-referential processes are accompanied by positive emotion and are associated with enhanced alpha activity in the posterior DMN hub, whereas in more introverted, neurotic, and collectivistic individuals these processes are more associated with negative emotion and enhanced alpha activity in the anterior DMN hub.

Other frequency bands also made some contribution to the prediction of SRTS scores. Specifically, in the Study 2 sample, a theta component whose maximal activity was localized in the superior frontal gyrus was the second strongest predictor; in the Study 3 sample, a beta component which showed maximal activity in the postcentral gyrus and a delta component with maximal activity in the superior frontal gyrus added to the prediction of SRTS scores. Interestingly, the beta component, as well as above discussed alpha components, was positively associated with SRTS scores, whereas both the theta and the delta components showed negative associations. This is in line with existing evidence showing that alpha and beta oscillations appear to positively correlate with DMN (Jann et al., 2010; Mantini et al., 2007), whereas frontal theta oscillations show negative correlations (Scheeringa et al., 2008).

Some limitations of this study need to be discussed. We measured the inter-individual variability in the degree of spontaneous self-referential thought by means of a retrospective self-report questionnaire. This measure clearly has a number of well known weaknesses (see e.g., discussion in Buckner et al., 2008; Giambra, 1995; Smallwood and Schooler, 2006; Smallwood et al., 2004). It should be admitted however that for now the researchers do not have in their disposition an ideal measure of these mental processes. Only a combination of different approaches may help to elucidate which effects are due to the process of interest and which are explained by confounding variables. Therefore, further research using different methods of measuring the self-referential processes is needed. Pertinent to this question, although a careful verification by language experts of each STQ item was carried out, there always could be a doubt as to whether these items have been understood equally by Russian and Taiwanese participants. However, this difficulty is peculiar to each cross-cultural research using translated self-report measures. Some assurance could be derived from the fact that the STQ factor structure appeared very similar in Russian and Taiwanese samples (we did not perform a formal comparison of factor structure using confirmatory factor analysis though due to insufficient number of participants in the Taiwanese sample). Nevertheless, this largely unexpected cross-cultural finding clearly needs further verification using other instruments (e.g., measures of individualism–collectivism) and other populations (e.g., comparison of a typical Western with a typical Eastern population).

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