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The temporal structure of resting-state brain activity in the medial prefrontal cortex predicts self-consciousness



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ABSTRACT

Recent studies have demonstrated an overlap between the neural substrate of resting-state activity and self-related processing in the cortical midline structures (CMS). However, the neural and psychological mechanisms mediating this so-called "rest-self overlap" remain unclear. To investigate the neural mechanisms, we estimated the temporal structure of spontaneous/resting-state activity, e.g. its long-range temporal correlations or self-affinity across time as indexed by the power-law exponent (PLE). The PLE was obtained in resting-state activity in the medial prefrontal cortex (MPFC) and the posterior cingulate cortex (PCC) in 47 healthy subjects by functional magnetic resonance imaging (fMRI). We performed correlation analyses of the PLE and Revised Self-Consciousness Scale (SCSR) scores, which enabled us to access different dimensions of self-consciousness and specified rest-self overlap in a psychological regard. The PLE in the MPFC's resting-state activity correlated with private self-consciousness scores from the SCSR. Conversely, we found no correlation between the PLE and the other subscales of the SCSR (public, social) or between other resting-state measures, including functional connectivity, and the SCSR subscales. This is the first evidence for the association between the scale-free dynamics of resting-state activity in the CMS and the private dimension of self-consciousness. This finding implies the relationship of especially the private dimension of self with the temporal structure of resting-state activity.

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1. Introduction

A number of studies have shown that cortical midline structures (CMS) are important in self-related processing (Gillihan and Farah, 2005; Legrand and Ruby, 2009; Northoff and Bermpohl, 2004; Kelley et al., 2002; Northoff et al., 2006; Van der Meer et al., 2010). Interestingly, two key regions in the CMS, the medial prefrontal cortex (MPFC) and the posterior cingulate cortex (PCC), were shown to highly overlap with the default-mode network (DMN) with particularly high levels of spontaneous activity and functional connectivity during resting-state activity (Boly et al., 2008; Christoff et al., 2003; Golland et al., 2007; Gusnard and

Raichle, 2001; Wicker et al., 2003; Raichle et al., 2001; Schneider et al., 2008). Furthermore, studies have shown that regions involved in resting-state activity and self-related processing are spatially overlapped in the CMS at regional levels (D'Argembeau et al., 2005; Gusnard and Raichle, 2001; Schneider et al., 2008; Qin and Northoff, 2011; Whitfield-Gabrieli et al., 2011), as well as at cellular levels (Lipsman et al., 2014), and have recently been described as "rest-self overlap" (Bai et al., 2015). Therefore, high resting-state activity may correspond to continuous self-related processing even in the absence of specific stimuli or tasks (Schneider et al., 2008). Supporting this view, studies have indicated the association between resting-state activity and self-related processing that is beyond the regional overlap of the two. Specifically, in one study, different degrees of self-relatedness of pictures displayed to subjects have been shown to parametrically modulate subsequent resting-state signal changes in CMS regions including the MPFC and PCC (Schneider et al., 2008). In another

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study, evoked brain activity by self-referential stimuli has been shown to positively correlate with the amplitude of low-frequency fluctuations in resting-state activity within the CMS (Huang et al., 2014). Finally, a recent study revealed that the ascription of high or low self-relatedness to emotional pictures correlates with the level of pre-stimulus activity (Bai et al., 2015). However, the exact neuronal features of resting-state activity that are linked with self-related processing, and which might account for the rest-self overlap, remain unclear.

Experimentally, self-related processing is usually tested by applying self- versus non-self-related stimuli, which have been shown to induce differential degrees of neural activity, referred to as stimulus-induced or task-evoked activity (Kelley et al., 2002: Schneider et al., 2008; Modinos et al., 2011). While stimulus-induced activity can be investigated for its neural overlap with resting-state activity, another approach would be to test for psychological measures of self-relatedness, and to correlate them with resting-state activity. We took the latter approach, using the wellestablished Self-Consciousness Scale (SCS) (Fenigstein et al., 1975; Abe et al., 1996) to investigate the self in three proposed dimensions (private, public and social), which have not been taken into consideration in task-based paradigm. Items in the private selfconsciousness subscale focus on self-related thoughts and reflections, and therefore expected to be most relevant to this study; the public self-consciousness subscale targets self as a social object (Fenigstein et al., 1975); the social anxiety subscale indicates how much discomfort one feels when others are present (Abe et al., 1996). While the SCS has been widely used in psychology studies, specifically with respect to its relation to personality and behaviour (Fenigstein et al., 1975; Fenigstein, 1987), the relationship between the dimensions of self-consciousness, especially private self-consciousness, and the brain's spontaneous or resting-state activity remains to be studied. The concept of self is often characterized as including different components, such as physical, mental, and public-social components (Damasio, 2010; Fingelkurts and Fingelkurts, 2011). We take the mental component to refer to the private experience of a self, or an inner sense of self, while its public and social aspects concern its relationship to others and the environment. Most paradigms applying self-related stimuli, such as one's own name or trait adjectives, target specifically this private component (Kelley et al., 2002; Schneider et al., 2008; Modinos et al., 2011). Since these self-related stimuli result in activity in the cortical midline structures, one would expect resting-state measures in these regions to be specifically related to private rather than public or social dimension of SCSR.

Furthermore, a central feature of the self is its continuity across time (Klein, 2014). This continuity may be in some way related to analogous temporal continuity in the spontaneous brain activity, which can be characterized, for instance, by its scale-free dynamics. Scale-free dynamics, indicated by the power spectrum with the formula $P\alpha \mathbf{1}/f^{\beta}$, are widely observed in nature (Abraham, 1994; Goldberger et al., 2002). Scale-free properties index longrange temporal correlations (Palva et al., 2013), which can be understood as self-affinity (Hardstone et al., 2012). Moreover, recently, it has been argued that they are relevant in investigating brain activity (Bullmore et al., 2001; He et al., 2010). Increasing evidence has suggested that spontaneous brain activity can be characterized by scale-free dynamics or power-law spectra: from field potentials (Freeman and Zhai, 2009; Manning et al., 2009; Miller et al., 2009; Milstein et al., 2009; He et al., 2010; Linkenkaer-Hansen et al., 2001; Palva et al., 2013) to fMRI signals (He et al., 2010; He, 2011; Huang et al., 2015). Moreover, changes in scale-free brain activity have been shown among different brain regions and between resting-state and task activation (He et al., 2010). Changes have also been observed between awake and slow wave sleep states (Zempel et al., 2012), through development (Fransson et al., 2013), and in mental illnesses, such as anxiety (Tolkunov et al., 2010), autism (Lai et al., 2010), as well as schizophrenia (Rădulescu and Mujica-Parodi, 2014). Interestingly, scale-free dynamics of spontaneous brain activity have been linked with personality traits at a psychological level, e.g. extraversion (Lei et al., 2013) and trait impulsivity (Hahn et al., 2012). Taken together, these studies suggest that scale-free brain activity may also be involved in the rest-self overlap, which was the main target of this study.

The general aim of our study was to investigate the relationship between scale-free brain activity and self-consciousness as indexed by the Self-Consciousness Scale. For this purpose, we obtained resting-state brain activity by fMRI in a large cohort of healthy subjects (n=47). Specifically, we first localized the MPFC and PCC by resting-state functional connectivity analysis, and then measured the scale-free dynamics of the two regions using a power-law exponent calculation. Subjects were administered a revised version of the Self-Consciousness Scale (SCSR) (Scheier and Carver, 1985), which enabled us to investigate different dimensions of self-consciousness using its subscales. Correlation analysis was performed to associate the scale-free dynamics and selfconsciousness. In addition, we performed several confirmation and control analyses: 1) we examined if our results were robust to different smoothing parameters when calculating the power spectrum of the BOLD signal; 2) we tested whether our results were consistent for the first 3 and last 3 min, as the PLE may change over time (Wink et al., 2008); 3) we confirmed our results by using another well-established method for the investigation of scale-free behaviour, namely detrended fluctuation analysis (DFA) (Linkenkaer-Hansen et al., 2001, 2005; He, 2011); and 4) we calculated other resting-state measures such as FC, regional homogeneity (ReHo), SD, and degree of centrality (DC) to explore the specificity of the functional relevance of resting-state's self-affine temporal structure (e.g. PLE) to self-consciousness.

2. Methods

2.1. Subjects

Forty seven right-handed subjects (26 females; ages 18–29) were recruited in this study. None had a history of major psychiatric or neurological disorders. Written informed consent was obtained from each subject before the experiment. This study was approved by the ethics committees at both the University of Ottawa and the University of British Columbia. The data from one subject was rejected due to consecutive excessive movement during fMRI scanning.

2.2. The assessment of self-consciousness

Subjects were asked to evaluate sentences (22 in total, see Supplementary material) of the Self-Consciousness Scale: A Revised Version for Use with General Populations (SCSR) (Scheier and Carver, 1985). The scale consists of three subscales: private self-consciousness (9 sentences), public self-consciousness (7 sentences) and social anxiety (6 sentences). Private self-consciousness scores indicate "the tendency to think about and attend to the more covert, hidden aspects of self" (e.g. one's privately held feelings); scores of public self-consciousness indicate "the tendency to think about self-aspects that are matters of public display" (e.g. one's overt behaviour); and social anxiety scores are presumed to involve a certain kind of focus and reaction to public self-consciousness (Scheier and Carver, 1985). The subjects were asked to evaluate the sentences using a 4-point rating scale (e.g., 0=not at all like me, 3=a lot like me). The score of each subscale

was calculated according to the instructions of the SCSR (Scheier and Carver, 1985).

2.3. fMRI data acquisition

A Philips Achieva 3T scanner with a standard head coil was used to acquire gradient-echo EPI images of the whole brain (TR, 1.0 s; TE, 30 ms; 21 slices; slice thickness=6 mm; spacing=0; field of view=210 mm; flip angle= 76° ; image matrix: 64×64 ; voxel size: $3.28 \times 3.28 \times 6.00$ mm³; number of fMRI frames: 360). During the 6 min resting-state fMRI scan, subjects were instructed to relax, stay awake and keep their eyes closed. Eye-tracking during fMRI was not available, but off-line post-scan recordings ensured that subjects complied with these instructions. Time-locked cardiac and respiratory signals were recorded. High-resolution anatomical images were acquired at the end of the experiment. The SCSR questionnaire was administered after the resting-state scan. There was no other task in the scanner prior to resting-state data acquisition.

2.4. Data pre-processing

Pre-processing steps were implemented in AFNI (Cox, 1996; http://afni.nimh.nih.gov/afni). First, physiological noise correction consisted of removal of time-locked cardiac and respiratory artefacts using RETROICOR (Glover et al., 2000). Subsequent steps included: slice timing correction; rigid body correction/realignment within and across runs; co-registration with high-resolution anatomical images; spatial normalization into Talaraich stereotactic space (Talairach et al., 1988); resampling to $3 \times 3 \times 3 \text{ mm}^3$ voxels; de-trending and regressing out the estimated six parameters of head motion and mean time series from the white matter (WM) and cerebrospinal fluid (CSF) by linear regression to control for non-neural noise (Fox et al., 2005). The WM and CSF masks were eroded by one voxel (Chai et al., 2012) to minimize partial voluming with grey matter. The data was spatially smoothed with a 6 mm full-width at half-maximum isotropic Gaussian kernel.

2.5. Definition of regions of interest (ROIs)

According to our hypotheses, the scale-free dynamics of the activity in two key regions in the CMS, the MPFC and PCC, were expected to show a close relationship with self-consciousness. Thus, we first localized the MPFC and PCC by a traditional restingstate functional connectivity analysis (Fox et al., 2005, 2006; Greicius et al., 2003, 2009; Laird et al., 2009; De Pasquale et al., 2012), since the two regions have been shown to be highly connected in the DMN (Fox et al., 2005; Greicius et al., 2003, 2009; De Pasquale et al., 2012). Specifically, we used a seed region in the PCC with 12 mm diameter (spherical) centerd on a previously published focus (Talairach coordinates: [-4, -52, 22], Laird et al., 2009). Next, voxel-wise FC maps were computed as maps of temporal correlation coefficients between the BOLD time course in each voxel and the BOLD time course averaged across voxels in the seed region in the traditional frequency band (0.01-0.08 Hz) (Biswal et al., 1995; Fox and Raichle, 2007; Zhang and Raichle, 2010). Contrast images were created for each subject then transformed into Fisher's Z for second-level one-sample t-tests. The group FC map of the MPFC and PCC was defined as voxels at threshold p < 0.001 (corrected, cluster extent > 100 voxels) (Fox et al., 2005, 2006; Greicius et al., 2003).

2.6. Calculation of power-law exponent

Scale-free dynamics are mathematically characterized by a power spectrum following the formula $P \propto 1/f^{\beta}$, where P is power, f

is frequency, and β is called the "power-law exponent (PLE)" (Bullmore et al., 2001). After pre-processing, the time course per voxel was normalized to zero mean and unit variance (z-value) (Stephens et al., 2013). As the variance is equal across all ROIs, all spectra have the same integrated area. Using methods previously optimized for fMRI (Rubin et al., 2013), the normalized power spectrum of the fMRI signal was computed for each voxel using AFNI program: 3dPeriodogram. The power spectrum of the BOLD signal was further smoothed with a Hamming window of 15 neighbouring frequency bins. In the next step, the averaged power spectra across voxels within each of the two ROIs, the MPFC and PCC, were extracted for each subject. The power spectrum was fitted with a power-law function $P \propto 1/f^{\beta}$ using a least-square estimation (in a log frequency by log power plot) in the frequency range of 0.01-0.2 Hz (Baria et al., 2013). Finally, the power-law exponent, β , of each subject's ROI was defined as the slope of the linear regression of log-power on log-frequency corresponding to the straight-line regime.

2.7. Correlation between scale-free property and self-consciousness

To establish the association between scale-free dynamics and self-consciousness, we performed partial correlation analyses (subject-based) with a 95% confidence interval (CI) based on 1000 bootstrap samples between PLE and scores of each of the SCSR self-consciousness subscales (private, public, and social anxiety). Due to the inter-correlation between subscales observed in our data (Supplementary Fig. 1) and a previous study (Scheier and Carver, 1985), each partial correlation analysis (e.g. correlating PLE and private) included the other two subscales as controlling factors (e.g. public and social). This yielded three correlations for each region, i.e. PLE-private, PLE-public, PLE-social. A Bonferroni correction for multiple comparisons was performed across the above six different correlations, such that only p values (before correction) below 0.0083 were considered as significant.

2.8. Control analysis

First, we were interested in the slope of the linear regression of log-power on log-frequency of the power spectrum of the BOLD signal (i.e. PLE) rather than the variations (or "noise") between neighbouring frequency bins. Thus, we applied additional smoothing on the power spectrum to reduce this noise and to improve linear fitting. As a result, however, it was also necessary to examine whether different smoothing parameters impacted our results. Thus, we compared the results by using different Hamming window sizes (HW=0, 3, 9, and 15).

Second, as scale-free dynamics are not necessarily stationary and the PLE may change over time (Wink et al., 2008), we examined if our results are consistent between the first 3 and last 3 min

Third, to avoid any bias in methods selection when investigating the scale-free behaviour, we re-calculated all above correlations by using the Hurst exponent (H) instead of the PLE. The H was calculated by a standard detrended fluctuation analysis (DFA) (Linkenkaer-Hansen et al., 2001, 2005; He, 2011). Specifically, the DFA measures the scaling of the root-mean-square fluctuation of the integrated and linearly detrended signals, F(T), as a function of time window size, T. The fluctuation F(T) is of the form $F(T) = T^H$, where H is the scaling exponent. Window sizes from 5 to 180 fMRI frames were chosen, and the number of total frames (360) is always an integer multiple of the window size.

Lastly, to explore the specificity of the functional relevance of the resting-state's self-affine temporal structure (as indexed by the PLE) to self-consciousness, we used four other common restingstate measures from the literature, including FC (Fox et al., 2005, 2006; Greicius et al., 2003, 2009; Laird et al., 2009, De Pasquale et al., 2012), regional homogeneity (ReHo) (Zang et al., 2004), temporal variability (SD) (Garrett et al., 2010, 2011) and degree of

centrality (DC) (Buckner et al., 2009; Di Martino et al., 2013; Zuo et al., 2012). Correlation analysis between these and the self-consciousness scores was performed in the same way as described

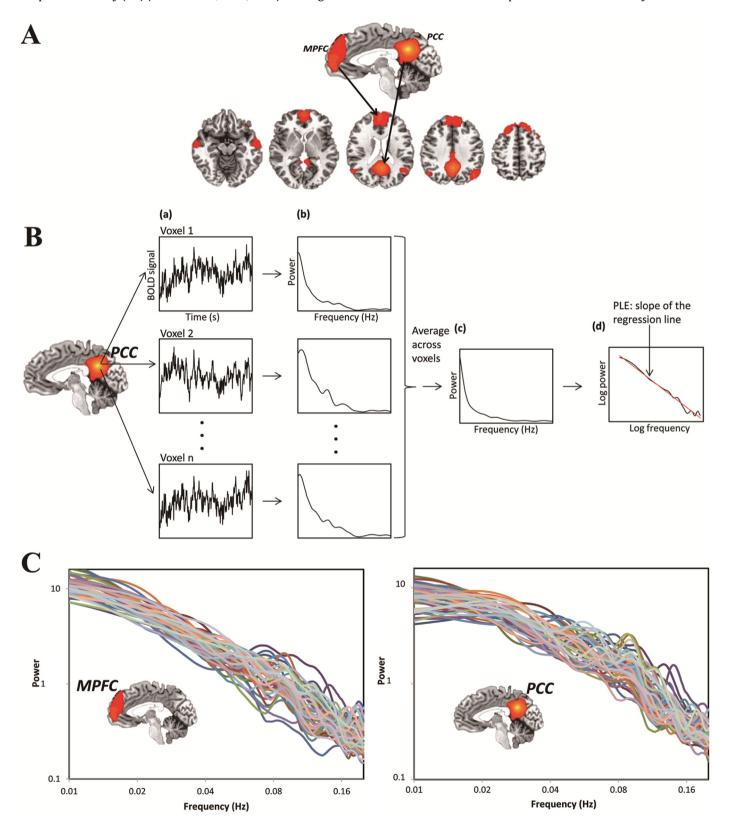


Fig. 1. A. The default-mode network was identified by resting-state functional connectivity analysis using the PCC as a seed region. Two cortical midline regions, the MPFC and PCC, were defined as regions of interest (ROIs). B. The procedure of calculating the power-law exponent (PLE) in a given ROI (e.g. PCC). (a) BOLD signals from three example voxels in the PCC; (b) power spectrum of the BOLD signal for each voxel; (c) The power spectra were averaged across voxels in the PCC; (d) The power-law exponent (PLE) was defined as the slope of the linear regression of log-power on log-frequency corresponding to the straight-line regime. C. The power spectra of all subjects in the MPFC and PCC. Different coloured lines represent individual subjects.

above (see Supplementary Methods).

3. Results

3.1. The spatial patterns of the DMN

The spatial patterns of the DMN that we obtained are in agreement with previous studies (Greicius et al., 2003; Fox et al., 2005; Fransson, 2005; Dosenbach et al., 2007; Seeley et al., 2007; Fox and Raichle, 2007; Mason et al., 2007), including the medial prefrontal cortex (MPFC), the posterior cingulate cortex (PCC), the bilateral temporo-parietal junction (TPJ) and the bilateral inferior temporal gyrus (ITG) (Fig. 1A). Two of these regions located in the CMS, the MPFC and PCC, are defined as our ROIs based on our primary hypothesis about self-rest overlap.

3.2. The PLE values

The PLE values across subjects (n=47) in the MPFC (mean=1.37; SD=0.18) and PCC (mean=1.34; SD=0.17) (Fig. 1B and C) are in accordance with previous studies $(He, 2011; Lei \ et \ al., 2013; Tagliazucchi \ et \ al., 2013)$. No significant difference of the mean PLE was observed between the MPFC and PCC at the group level (p=0.3).

3.3. Correlation between the PLE and SCSR

Significant correlation between the PLE and SCSR was observed only for the private self-consciousness subscale in the MPFC (PLE-Private; $r\!=\!0.413$, $p\!=\!0.005$; remaining significant with Bonferroni correction). Furthermore, the correlation coefficient of PLE-Private was significantly different from the absolute correlation coefficient of both PLE-Public ($z\!=\!3.43$, $p\!=\!0.0003$) and PLE-Social ($z\!=\!2.64$, $p\!=\!0.0041$) in the MPFC. No significant correlation between the

PLE and SCSR was observed for either PLE-Public or PLE-Social in the MPFC, or between the PLE and subscales of SCSR in the PCC (Fig. 2 and Table S1).

To confirm the above correlation results, we further divided the subject group by median split into high- and low-score groups according to the individual scores on three subscales. As expected, for private self-consciousness, there was a significant difference between high- and low-score groups for the PLE in the MPFC; this was tested using a two-sample t-test (t=2.73, p=0.009).

3.4. Results of control analysis

We applied different smoothing parameters, more specifically, varying Hamming window sizes (HW=0, 3, 9, and 15), to test the robustness of our results. The smoothness of the power-spectrum was increased by enlarging the HW (Fig. 3A). However, the correlation of PLE-Private in the MPFC was not affected by different HMs (Table 1). Moreover, consistent results were seen for the first and last 3 min data (Fig. 3B and Table 1).

To avoid any bias in methods selection when investigating the scale-free behaviour, we re-calculated all above correlations using the Hurst exponent (H). Again, the correlation between H and private self-consciousness (r=0.392, p=0.008; remaining significant with Bonferroni correction) was the only significant one among all the correlations between H and SCSR in both MPFC and PCC (Fig. 4). As a proof of principle, the PLE and H were highly correlated with each other in both MPFC (r=0.58, p<0.001) and PCC (r=0.46, p=0.001).

Finally, we performed a control analysis with other restingstate measures (FC, ReHo, SD and DC). No significant correlation between any of the resting-state measures and SCSR was observed (see Supplementary methods and Table S1).

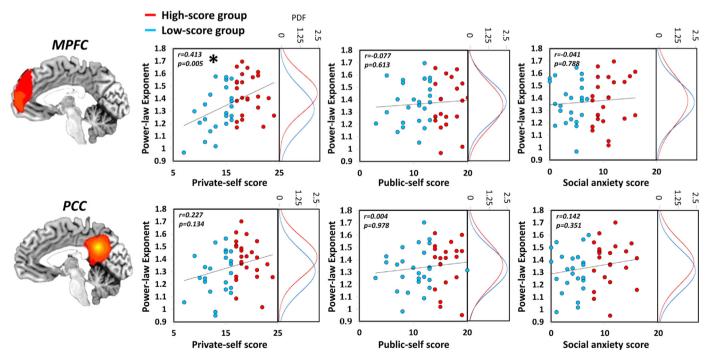


Fig. 2. Scatter plots displaying the relationship between SCSR scores and the power-law exponent (PLE) in the MPFC and PCC. Correlations were calculated for PLE and private self-consciousness (left), public self-consciousness (middle), and social anxiety (right). A significant correlation was observed between private self-consciousness and PLE in the MPFC (p=0.005; remaining significant with Bonferroni correction among six correlations). The curves to the right of the scatter plots display the distribution of the subjects' PLE divided into high- (red), and low-score (blue) groups. PDF: Probability density function, indicating the relative likelihood for the PLE to take on a given value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

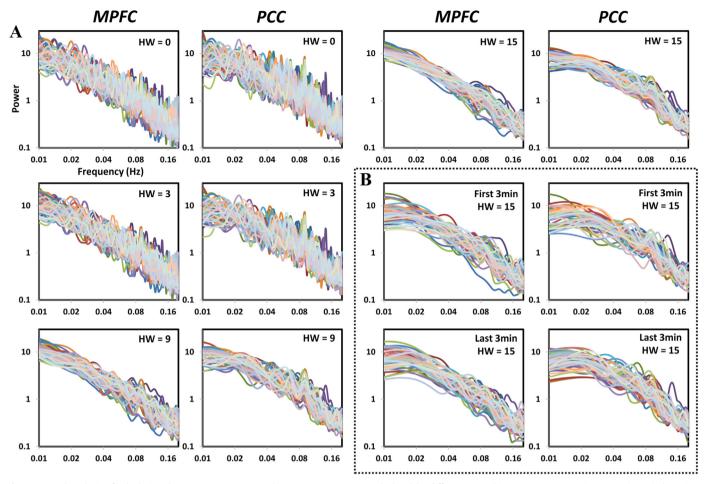


Fig. 3. Control analysis of calculating the power spectrum. A. The power spectra were calculated by different smoothing parameters, varying Hamming window sizes (HW=0, 3, 9, and 15), in the MPFC and PCC. B. Comparing the power spectra for the first and last 3 min data. Different coloured lines represent individual subjects.

 Table 1

 Statistics of the correlations between the PLE and SCSR.

	Private		Public		Social	
	MPFC	PCC	MPFC	PCC	MPFC	PCC
HW=0	*r=0.427	r=0.257	r = -0.086	r = -0.008	r=0.052	r=0.131
	p = 0.003	p = 0.087	p = 0.575	p = 0.960	p = 0.734	p = 0.392
HW=3	r = 0.430	r=0.258	r = -0.092	r = -0.009	r=0.050	r=0.128
	p = 0.003	p = 0.087	p = 0.550	p = 0.954	p = 0.746	p = 0.403
HW=9	r = 0.424	r=0.238	r = -0.086	r = -0.009	r = 0.040	r=0.136
	p = 0.004	p = 0.115	p = 0.572	p = 0.953	p = 0.795	p = 0.373
HW=15	r = 0.413	r=0.227	r = -0.077	r = 0.004	r = 0.041	r = 0.142
	p = 0.005	p = 0.134	p = 0.613	p = 0.978	p = 0.788	p = 0.351
First 3 min (HW=15)	r = 0.313	r = 0.068	r = -0.061	r = -0.064	r = 0.050	r = 0.205
	p = 0.036	p = 0.658	p = 0.689	p = 0.675	p = 0.745	p = 0.176
Last 3 min (HW=15)	r = 0.454	r=0.339	r = -0.141	r = 0.027	r=0.161	r = 0.177
	p = 0.002	p = 0.023	p = 0.354	p = 0.861	p = 0.291	p = 0.245

HW: Hamming window size.

4. Discussion

In the present study, we aimed to investigate the association between the scale-free dynamics of resting-state fMRI activity, as indexed by the power-law exponent (PLE), and different dimensions of self-consciousness at a psychological level. We found a significant positive correlation between the PLE in the MPFC and private self-consciousness. This result suggests that higher degrees of long-range temporal correlations (as signified by the PLE) are specifically related to higher degrees of private self-consciousness.

To our knowledge, the present study provides, for the first time, evidence that scale-free properties of resting-state fluctuations, especially in the MPFC, are associated with a private dimension of self (private self-consciousness).

The MPFC is a region that has been closely linked to self-related processing (D'Argembeau, 2013; Gillihan and Farah, 2005; Kelley et al. 2002; Northoff et al. 2006; Northoff and Bermpohl, 2004; Supekar et al., 2010; van der Meer et al., 2010). Usually, self-related activity in the MPFC has been detected by looking at different levels of neuronal activity during self- and non-self-related stimuli

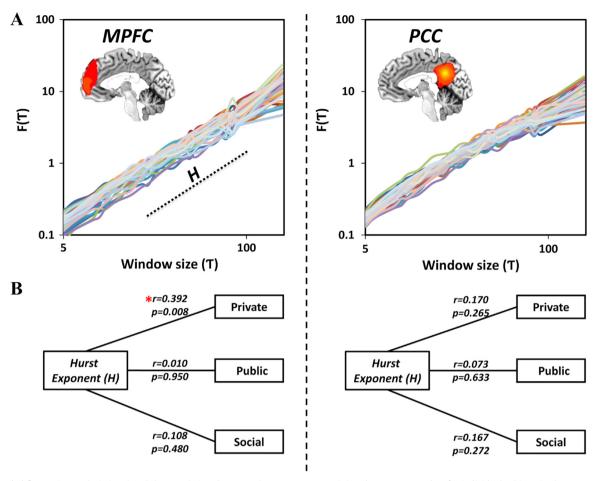


Fig. 4. Detrended fluctuation analysis (DFA) and the correlations between the Hurst exponent (*H*) and SCSR. A. DFA plots for individual subjects in the MPFC and PCC. The fluctuation, *F*(T), is computed at different time window size, T, and plotted in double-logarithmic scales. The scaling exponent, *H*, is the slope of linear regression. B. The relationship between SCSR scores and *H* in the MPFC and PCC. A significant correlation was observed between private self-consciousness and *H* in the MPFC.

(Kelley et al., 2002; Schneider et al., 2008; Modinos et al. 2011; Huang et al., 2014). One's own name or trait adjectives are usually taken as self-related stimuli, which target a private component of self (Kelley et al., 2002; Schneider et al., 2008; Modinos et al., 2011). One would consequently assume that MPFC activity is mainly related to private self-consciousness rather than public or social dimensions of self. However, this remained to be investigated.

Our data provides first evidence in that direction. Private self-consciousness was the only dimension to correlate with the temporal structure of resting-state activity in the MPFC. In contrast, we did not observe any correlation of our various resting-state measures with the scores for public self-consciousness or social anxiety. These results suggest a specific association of the MPFC resting-state activity with private rather than public self-consciousness. Future studies may consider the link between self-related stimulus-induced activity and private self-consciousness at a psychological level. Since applying self-related stimuli, such as one's own name or trait adjectives, reflects a private aspect of self, one would expect the resulting self-related stimulus-induced activity to correlate with private self-consciousness specifically. This remains to be tested in the future.

Why and how is MPFC resting-state activity related to private self-consciousness? Previous studies demonstrated the MPFC's involvement in both self-related processing and high resting-state activity (D'Argembeau et al., 2005; Schneider et al., 2008; Qin and Northoff, 2011; Whitfield-Gabriel et al., 2011). However, the exact psychological and neural mechanisms that mediate this rest-self

overlap are unclear. Our correlation between resting-state activity and private self-consciousness lends further support to the observed rest-self overlap (Bai et al., 2015) by providing a clue concerning a possible mechanism, namely the long-range temporal correlations with the temporal structure of spontaneous activity. Moreover, our results specify that, in a psychological regard, only scores of private self-consciousness correlated with resting-state activity. In contrast, no correlation was found with either public self-consciousness or social anxiety. More generally, this suggests that some individually specific information about the private or individual self (rather than its public or social aspects) is encoded in the resting-state brain activity.

How is the private self-specific information encoded into the resting-state activity of the MPFC? We here investigated different measures of resting-state activity, including the power-law exponent (PLE), regional homogeneity (ReHo), temporal variability (SD), degree of centrality (DC), and functional connectivity (FC). Scale-free activity, as indicated by the PLE and confirmed by the Hurst exponent (H), was the only neural measure to correlate. As the PLE and H measure specifically the temporal structure of spontaneous activity, rather than signal synchrony across regions (e.g. ReHo, DC, and FC) or the overall power of signal fluctuations (e.g. SD), this may suggest that the rest-self overlap in the MPFC is mediated by the temporal structure of the spontaneous activity. Therefore, we tentatively hypothesize that the resting-state's neuronal self-affinity translates in some yet unclear way into psychological self-relatedness as manifest in private self-consciousness. In other words, the degree of long-range temporal correlations, which describe the diachronic aspect of the spontaneous activity, may be translated into the diachronic features of the self on the psychological level (Fingelkurts and Fingelkurts, 2011; Fingelkurts et al., 2013). If this were the case, one would expect some degree of temporal correspondence between the temporal structure on the neuronal level, including its degree of autocorrelation across time, and the degree of self-consistency across time.

Our finding is in line with a recent study, in which researchers found a higher degree of scale-free dynamics was related to a lower degree of extraversion (Lei et al., 2013). A lower degree of extraversion (or a higher degree of introversion) could be indicative of a higher degree of private self-consciousness, thereby aligning with our findings that higher private self-consciousness scores correlate positively with the PLE.

We are aware of some limitations in our approach. The possible association between scale-free dynamics and the encoding of a private dimension of self in the resting-state must be confirmed by more observations, such as how resting-state activity interacts with the task-evoked activity (Huang et al., 2015). Currently, it remains unclear how the PLE changes during self-related tasks. Since a larger PLE has been observed during resting-state activity compared with task-evoked activity (He, 2011), one would expect the PLE during the self-related task to be attenuated when compared with resting-state activity. Based on the observed correspondence of higher PLE with higher sense of self in the private dimension, we assume that the PLE will be less attenuated during self-related tasks versus non-self-related tasks.

Another limitation is that self and consciousness were not experimentally dissociated. Previous studies implied that the PLE and level of consciousness are associated with each other, based on the association between the PLE and slow cortical potentials (He et al., 2010; He and Raichle, 2009) and change in scale-free dynamics between awake and sleep states (Zempel et al., 2012). However, in our study self and consciousness confound. From our results, we are not certain if the PLE is directly related to the self, consciousness or both. Future studies may attempt to disentangle self and consciousness and investigate the unconscious or implicit processing of self-related stimuli and their relation to resting-state activity.

Lastly, we used a relatively short repetition time (TR=1~s) of fMRI scanning, which was due to the consideration that higher temporal resolution is beneficial when computing power spectrum of the BOLD signal. A short TR, however, lowers the signal-tonoise ratio (SNR) and spatial resolution, in turn potentially affecting other common measures, such as functional connectivity or ReHo. As a result, we cannot completely rule out the possibility that other measures may be also associated with self-consciousness when a longer TR is applied (e.g. TR=2~s). Also, the PLE does not appear to be the only informative measure since several correlations between resting-state measures other than the PLE and SCSR were almost significant (FC and DC with the Social subscale; see Supplementary Table S1). Therefore, it remains to be determined in future studies if the private self-consciousness subscale is solely associated with PLE.

In summary, we demonstrate for the first time a direct relationship between the resting-state's scale-free activity and its temporal structure in the MPFC with private self-consciousness. This significantly extends previous findings of rest-self overlap, indicating self-relatedness to be encoded in especially the temporal structure of the MPFC resting-state activity. The self-affine nature of the MPFC resting-state activity seems to translate into self-relatedness (and ultimately self-consciousness) at a psychological level.

Conflict of interest

None declared.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia. 2016.01.025.

References

- Abe, S., Bagozzi, R.P., Sadarangani, P., 1996. An investigation of construct validity and generalizability of the self-concept. J. Int. Consum. Mark. 8 (3–4), 97–123. http://dx.doi.org/10.1300/J046v08n03_06.
- Abraham, R.H., 1994. Fractals, chaos, power laws: minutes from an infinite paradise. J. Econ. Dyn. Control . http://dx.doi.org/10.1016/0165-1889(94)90045-0.
- Bai, Y., Nakao, T., Xu, J., Qin, P., Chaves, P., Heinzel, A., Northoff, G., 2015. Resting state glutamate predicts elevated pre-stimulus alpha during self-relatedness—a combined EEG-MRS study on "rest-self overlap. Soc. Neurosci. http://dx.doi. org/10.1080/17470919.2015.1072582
- Baria, A.T., Mansour, A., Huang, L., Baliki, M.N., Cecchi, G.A., Mesulam, M.M., Apkarian, A.V., 2013. Linking human brain local activity fluctuations to structural and functional network architectures. NeuroImage 73, 144–155. http://dx.doi.org/10.1016/j.neuroimage.2013.01.072.
- Biswal, B., Yetkin, F.Z., Haughton, V.M., Hyde, J.S., 1995. Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. Magn. Reson. Med. 34, 537–541. http://dx.doi.org/10.1002/mrm.1910340409.
- Boly, M., Phillips, C., Tshibanda, L., Vanhaudenhuyse, A., Schabus, M., Dang-Vu, T.T., Laureys, S., 2008. Intrinsic brain activity in altered states of consciousness: how conscious is the default mode of brain function? Ann. N. Y. Acad. Sci. 1129, 119–129. http://dx.doi.org/10.1196/annals.1417.015.
- Buckner, R.L., Sepulcre, J., Talukdar, T., Krienen, F.M., Liu, H., Hedden, T., Johnson, K. A., 2009. Cortical hubs revealed by intrinsic functional connectivity: mapping, assessment of stability, and relation to Alzheimer's disease. J. Neurosci. 29, 1860–1873. http://dx.doi.org/10.1523/JNEUROSCI.5062-08.2009.
- Bullmore, E., Long, C., Suckling, J., Fadili, J., Calvert, G., Zelaya, F., Brammer, M., 2001. Colored noise and computational inference in neurophysiological (fMRI) time series analysis: resampling methods in time and wavelet domains. Hum. Brain Mapp. 12, 61–78. http://dx.doi.org/10.1002/1097-0193(200102)12:2 < 61::AID-HBM1004 > 3.0.CO;2-W.
- Chai, X.J., Castañán, A.N., Öngür, D., Whitfield-Gabrieli, S., 2012. Anticorrelations in resting state networks without global signal regression. NeuroImage 59, 1420–1428. http://dx.doi.org/10.1016/j.neuroimage.2011.08.048.
- Christoff, K., Ream, J.M., Geddes, L.P.T., Gabrieli, J.D.E., 2003. Evaluating self-generated information: anterior prefrontal contributions to human cognition. Behav. Neurosci. 117, 1161–1168. http://dx.doi.org/10.1037/0735-7044.117.6.1161.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Comput. Biomed. Res. Int. J. 29, 162–173. http://dx.doi.org/10.1006/cbmr.1996.0014.
- D'Argembeau, A., 2013. On the role of the ventromedial prefrontal cortex in self-processing: the valuation hypothesis. Front. Hum. Neurosci. 7, 372. http://dx.doi.org/10.3389/fnhum.2013.00372.
- D'Argembeau, A., Collette, F., Van Der Linden, M., Laureys, S., Del Fiore, G., Degueldre, C., Salmon, E., 2005. Self-referential reflective activity and its relationship with rest: a PET study. NeuroImage 25, 616–624. http://dx.doi.org/10.1016/j.neuroimage.2004.11.048.
- Damasio, A., 2010. Self comes to mind. Human Nature (p. 367). [Retrieved from] \(\hat{ttp://books.google.com/books?id=AuNjhF6HYIkC&pgis=1}\).
- De Pasquale, F., Della Penna, S., Snyder, A.Z., Marzetti, L., Pizzella, V., Romani, G.L., Corbetta, M., 2012. A cortical core for dynamic integration of functional networks in the resting human brain. Neuron 74 (4), 753–764. http://dx.doi.org/10.1016/j.neuron.2012.03.031.

- Di Martino, A., Zuo, X.N., Kelly, C., Grzadzinski, R., Mennes, M., Schvarcz, A., Milham, M.P., 2013. Shared and distinct intrinsic functional network centrality in autism and attention-deficit/hyperactivity disorder. Biol. Psychiatry 74, 623–632. http://dx.doi.org/10.1016/j.biopsych.2013.02.011.
- Dosenbach, N.U.F., Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., Dosenbach, R.A. T., Petersen, S.E., 2007. Distinct brain networks for adaptive and stable task control in humans. Proc. Natl. Acad. Sci. USA 104, 11073–11078. http://dx.doi.org/10.1073/pnas.0704320104.
- Fenigstein, A., Scheier, M.F., Buss, A.H., 1975. Public and private self-consciousness: assessment and theory. J. Consult. Clin. Psychol. 43 (4), 522–527. http://dx.doi. org/10.1037/h0076760.
- Fenigstein, A., 1987. On the nature of public and private self-consciousness. J. Personal. 55, 543–554. http://dx.doi.org/10.1111/j.1467-6494.1987.tb00450.x.
- Fingelkurts, A.A., Fingelkurts, A.A., 2011. Persistent operational synchrony within brain default-mode network and self-processing operations in healthy subjects. Brain Cogn. 75 (2), 79–90. http://dx.doi.org/10.1016/j.bandc.2010.11.015.
- Fingelkurts, A.A., Fingelkurts, A.A., Neves, C.F.H., 2013. Consciousness as a phenomenon in the operational architectonics of brain organization: criticality and self-organization considerations. Chaos Solitons Fractals 55, 13–31. http://dx.doi.org/10.1016/j.chaos.2013.02.007.
- Fox, M.D., Corbetta, M., Snyder, A.Z., Vincent, J.L., Raichle, M.E., 2006. Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. Proc. Natl. Acad. Sci. USA 103, 10046–10051. http://dx.doi.org/10.1073/pnas.0604187103.
- Fox, M.D., Raichle, M.E., 2007. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nat. Rev. Neurosci. 8, 700–711. http://dx.doi.org/10.1038/nrn2201.
- Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C., Raichle, M.E., 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. USA 102, 9673–9678. http://dx.doi. org/10.1073/pnas.0504136102.
- Fransson, P., 2005. Spontaneous low-frequency BOLD signal fluctuations: an fMRI investigation of the resting-state default mode of brain function hypothesis. Hum. Brain Mapp. 26, 15–29. http://dx.doi.org/10.1002/hbm.20113.
- Fransson, P., Metsäranta, M., Blennow, M., Åden, U., Lagercrantz, H., Vanhatalo, S., 2013. Early development of spatial patterns of power-law frequency scaling in FMRI resting-state and EEG data in the newborn brain. Cereb. Cortex 23 (3), 638–646. http://dx.doi.org/10.1093/cercor/bhs047.
- Freeman, W.J., Zhai, J., 2009. Simulated power spectral density (PSD) of background electrocorticogram (ECoG). Cogn. Neurodynamics 3, 97–103. http://dx.doi.org/10.1007/s11571-008-9064-y.
- Garrett, D.D., Kovacevic, N., McIntosh, A.R., Grady, C.L., 2010. Blood oxygen level-dependent signal variability is more than just noise. J. Neurosci. 30, 4914–4921. http://dx.doi.org/10.1523/JNEUROSCI.5166-09.2010.
- Garrett, D.D., Kovacevic, N., McIntosh, A.R., Grady, C.L., 2011. The importance of being variable. J. Neurosci. 31, 4496–4503. http://dx.doi.org/10.1523/ JNEUROSCI.5641-10.2011.
- Gillihan, S.J., Farah, M.J., 2005. Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. Psychol. Bull. 131, 76–97. http://dx.doi.org/10.1037/0033-2909.131.1.76.
- Glover, G.H., Li, T.Q., Ress, D., 2000. Image-based method for retrospective correction of physiological motion effects in fMRI: RETROICOR. Magn. Reson. Med. 44, 162–167. http://dx.doi.org/10.1002/1522-2594(200007)44:1 < 162::AID-MRM23 > 3.0.CO:2-E.
- Goldberger, A.L., Amaral, L.A.N., Hausdorff, J.M., Ivanov, P.C., Peng, C.-K., Stanley, H. E., 2002. Fractal dynamics in physiology: alterations with disease and aging. Proc. Natl. Acad. Sci. USA 99 (Suppl. 1), S2466–S2472. http://dx.doi.org/10.1073/pnas.012579499
- Golland, Y., Bentin, S., Gelbard, H., Benjamini, Y., Heller, R., Nir, Y., Malach, R., 2007. Extrinsic and intrinsic systems in the posterior cortex of the human brain revealed during natural sensory stimulation. Cereb. Cortex 17, 766–777. http://dx.doi.org/10.1093/cercor/bhk030.
- Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc. Natl. Acad. Sci. USA 100 (1), 253–258. http://dx.doi.org/10.1073/pnas.0135058100.
- Greicius, M.D., Supekar, K., Menon, V., Dougherty, R.F., 2009. Resting-state functional connectivity reflects structural connectivity in the default mode network. Cereb. Cortex 19, 72–78. http://dx.doi.org/10.1093/cercor/bhn059.
- Gusnard, D.A., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. Nat. Rev. Neurosci. 2, 685–694. http://dx.doi.org/10.1038/35094500.
- Hahn, T., Dresler, T., Ehlis, A.-C., Pyka, M., Dieler, A.C., Saathoff, C., Fallgatter, A.J., 2012. Randomness of resting-state brain oscillations encodes Gray's personality trait. NeuroImage 59 (2), 1842–1845. http://dx.doi.org/10.1016/j. neuroimage.2011.08.042.
- Hardstone, R., Poil, S.-S., Schiavone, G., Jansen, R., Nikulin, V.V., Mansvelder, H.D., Linkenkaer-Hansen, K., 2012. Detrended fluctuation analysis: a scale-free view on neuronal oscillations. Front. Physiol. 3, 450. http://dx.doi.org/10.3389/ fphys.2012.00450.
- He, B.J., 2011. Scale-free properties of the functional magnetic resonance imaging signal during rest and task. J. Neurosci. http://dx.doi.org/10.1523/ JNEUROSCI.2111-11.2011.
- He, B.J., Raichle, M.E., 2009. The fMRI signal, slow cortical potential and consciousness. Trends Cogn. Sci. 13, 302–309. http://dx.doi.org/10.1016/j.tics.2009.04.004.
- He, B.J., Zempel, J.M., Snyder, A.Z., Raichle, M.E., 2010. The temporal structures and

- functional significance of scale-free brain activity. Neuron 66 (3), 353–369. http://dx.doi.org/10.1016/j.neuron.2010.04.020.
- Huang, Z., Dai, R., Wu, X., Yang, Z., Liu, D., Hu, J., Northoff, G., 2014. The self and its resting state in consciousness: an investigation of the vegetative state. Hum. Brain Mapp. 35, 1997–2008. http://dx.doi.org/10.1002/hbm.22308.
- Huang, Z., Zhang, J., Longtin, A., Dumont, G., Duncan, N.W., Pokorny, J., Northoff, G., 2015. Is there a nonadditive interaction between spontaneous and evoked activity? Phase-dependence and its relation to the temporal structure of scalefree brain activity. Cereb. Cortex, 1–23. http://dx.doi.org/10.1093/cercor/ bhv288.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. J. Cogn. Neurosci. 14, 785–794. http://dx.doi.org/10.1162/08989290260138672.
- Klein, S.B., 2014. Sameness and the self: philosophical and psychological considerations. Front. Psychol., 5. http://dx.doi.org/10.3389/fpsyg.2014.00029.
- Lai, M.-C., Lombardo, M.V., Chakrabarti, B., Sadek, S.A., Pasco, G., Wheelwright, S.J., Suckling, J., 2010. A shift to randomness of brain oscillations in people with autism. Biol. Psychiatry 68 (12), 1092–1099. http://dx.doi.org/10.1016/j. biopsych.2010.06.027.
- Laird, A.R., Eickhoff, S.B., Li, K., Robin, D.A., Glahn, D.C., Fox, P.T., 2009. Investigating the functional heterogeneity of the default mode network using coordinatebased meta-analytic modeling. J. Neurosci. 29 (46), 14496–14505. http://dx.doi. org/10.1523/INEUROSCI.4004-09.2009.
- Legrand, D., Ruby, P., 2009. What is self-specific? Theoretical investigation and critical review of neuroimaging results. Psychol. Rev. 116, 252–282. http://dx. doi.org/10.1037/a0014172.
- Lei, X., Zhao, Z., Chen, H., 2013. Extraversion is encoded by scale-free dynamics of default mode network. NeuroImage 74, 52–57. http://dx.doi.org/10.1016/j. neuroImage.2013.02.020.
- Linkenkaer-Hansen, K., Nikouline, V.V., Palva, J.M., Ilmoniemi, R.J., 2001. Long-range temporal correlations and scaling behavior in human brain oscillations. J. Neurosci. 21 (4), 1370–1377.
- Linkenkaer-Hansen, K., Monto, S., Rytsälä, H., Suominen, K., Isometsä, E., Kähkönen, S., 2005. Breakdown of long-range temporal correlations in theta oscillations in patients with major depressive disorder. J. Neurosci. 25 (44), 10131–10137. http://dx.doi.org/10.1523/JNEUROSCI.3244-05.2005.
- Lipsman, N., Nakao, T., Kanayama, N., Krauss, J.K., Anderson, A., Giacobbe, P., Northoff, G., 2014. Neural overlap between resting state and self-relevant activity in human subcallosal cingulate cortex—single unit recording in an intracranial study. Cortex 60, 139–144. http://dx.doi.org/10.1016/j. cortex.2014.09.008.
- Manning, J.R., Jacobs, J., Fried, I., Kahana, M.J., 2009. Broadband shifts in local field potential power spectra are correlated with single-neuron spiking in humans. J. Neurosci. 29, 13613–13620. http://dx.doi.org/10.1523/JNEUROSCI.2041-09.2009.
- Mason, M.F., Norton, M.I., Van Horn, J.D., Wegner, D.M., Grafton, S.T., Macrae, C.N., 2007. Wandering minds: stimulus-independent thought. Science 315, 393–395. http://dx.doi.org/10.1126/science.1131295.
- Miller, K.J., Zanos, S., Fetz, E.E., den Nijs, M., Ojemann, J.G., 2009. Decoupling the cortical power spectrum reveals real-time representation of individual finger movements in humans. J. Neurosci. 29, 3132–3137. http://dx.doi.org/10.1523/ INFLIROSCI.5506-08.2009.
- Milstein, J., Mormann, F., Fried, I., Koch, C., 2009. Neuronal shot noise and Brownian 1/f2 behavior in the local field potential. PLoS One 4, e4338. http://dx.doi.org/10.1371/journal.pone.0004338.
- Modinos, G., Renken, R., Ormel, J., Aleman, A., 2011. Self-reflection and the psychosis-prone brain: an fMRI study. Neuropsychology 25, 295–305. http://dx. doi.org/10.1037/a0021747.
- Northoff, G., Bermpohl, F., 2004. Cortical midline structures and the self. Trends Cogn. Sci. http://dx.doi.org/10.1016/j.tics.2004.01.004.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain—a meta-analysis of imaging studies on the self. NeuroImage 31 (1), 440–457. http://dx.doi.org/10.1016/j.neuroImage.2005.12.002.
- Palva, J.M., Zhigalov, A., Hirvonen, J., Korhonen, O., Linkenkaer-Hansen, K., Palva, S., 2013. Neuronal long-range temporal correlations and avalanche dynamics are correlated with behavioral scaling laws. Proc. Natl. Acad. Sci. USA 110, 3585–3590. http://dx.doi.org/10.1073/pnas.1216855110.
- Qin, P., Northoff, G., 2011. How is our self related to midline regions and the default-mode network? NeuroImage 57 (3), 1221–1233. http://dx.doi.org/10.1016/j.neuroimage.2011.05.028.
- Rădulescu, A., Mujica-Parodi, L.R., 2014. Network connectivity modulates power spectrum scale invariance. NeuroImage 90, 436–448. http://dx.doi.org/10.1016/ j.neuroimage.2013.12.001.
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G. L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. USA 98, 676–682. http://dx.doi.org/10.1073/pnas.98.2.676.
- Rubin, D., Fekete, T., Mujica-Parodi, L.R., 2013. Optimizing complexity measures for fMRI data: algorithm, artifact, and sensitivity. PLoS One, 8. http://dx.doi.org/10.1371/journal.pone.0063448.
- Scheier, M.F., Carver, C.S., 1985. The self-consciousness scale: a revised version for use with general populations. J. Appl. Soc. Psychol. 15, 687–699. http://dx.doi. org/10.1111/j.1559-1816.1985.tb02268.x.
- Schneider, F., Bermpohl, F., Heinzel, A, Rotte, M., Walter, M., Tempelmann, C., Northoff, G., 2008. The resting brain and our self: self-relatedness modulates resting state neural activity in cortical midline structures. Neuroscience 157 (1),

- 120-131. http://dx.doi.org/10.1016/j.neuroscience.2008.08.014.
- Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. J. Neurosci. 27, 2349–2356. http://dx.doi.org/10.1523/INEUROSCI.5587-06.2007.
- Stephens, G.J., Honey, C.J., Hasson, U., 2013. A place for time: the spatiotemporal structure of neural dynamics during natural audition. J. Neurosci. 110. http://dx. doi.org/10.1152/jn.00268.2013.
- Supekar, K., Uddin, L.Q., Prater, K., Amin, H., Greicius, M.D., Menon, V., 2010. Development of functional and structural connectivity within the default mode network in young children. NeuroImage 52, 290–301. http://dx.doi.org/10.1016/j.neuroimage.2010.04.009.
- Tagliazucchi, E., von Wegner, F., Morzelewski, A., Brodbeck, V., Jahnke, K., Laufs, H., 2013. Breakdown of long-range temporal dependence in default mode and attention networks during deep sleep. Proc. Natl. Acad. Sci. USA 110, 15419–15424. http://dx.doi.org/10.1073/pnas.1312848110.
- Talairach, J., Tournoux, P., 1988. Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging. Neuropsychologia 39, 145. http://dx.doi.org/10.1111/mono.12083.
- Tolkunov, D., Rubin, D., Mujica-Parodi, L.R., 2010. Power spectrum scale invariance quantifies limbic dysregulation in trait anxious adults using fMRI: adapting methods optimized for characterizing autonomic dysregulation to neural dynamic time series. NeuroImage 50, 72–80. http://dx.doi.org/10.1016/j. neuroimage.2009.12.021.
- Van der Meer, L., Costafreda, S., Aleman, A., David, A.S., 2010. Self-reflection and the

- brain: a theoretical review and meta-analysis of neuroimaging studies with implications for schizophrenia. Neurosci. Biobehav. Rev. 34, 935–946.
- Whitfield-Gabrieli, S., Moran, J.M., Nieto-Castañón, A., Triantafyllou, C., Saxe, R., Gabrieli, J.D.E., 2011. Associations and dissociations between default and self-reference networks in the human brain. NeuroImage 55, 225–232. http://dx.doi.org/10.1016/j.neuroimage.2010.11.048.
- Wicker, B., Ruby, P., Royet, J.P., Fonlupt, P., 2003. A relation between rest and the self in the brain? Brain Res. Rev. 43 (2), 224–230. http://dx.doi.org/10.1016/j. brainresrev.2003.08.003.
- Wink, A.M., Bullmore, E., Barnes, A., Bernard, F., Suckling, J., 2008. Monofractal and multifractal dynamics of low frequency endogenous brain oscillations in functional MRI. Hum. Brain Mapp. 29 (7), 791–801. http://dx.doi.org/10.1002/ hbm 20593
- Zang, Y., Jiang, T., Lu, Y., He, Y., Tian, L., 2004. Regional homogeneity approach to fMRI data analysis. NeuroImage 22, 394–400. http://dx.doi.org/10.1016/j. neuroimage.2003.12.030.
- Zempel, J.M., Politte, D.G., Kelsey, M., Verner, R., Nolan, T.S., Babajani-Feremi, A., Larson-Prior, L.J., 2012. Characterization of scale-free properties of human electrocorticography in awake and slow wave sleep states. Front. Neurol. 3, 76. http://dx.doi.org/10.3389/fneur.2012.00076.
- Zhang, D., Raichle, M.E., 2010. Disease and the brain's dark energy. Nat. Rev. Neurol. 6, 15–28. http://dx.doi.org/10.1038/nrneurol.2009.198.
- Zuo, X.N., Ehmke, R., Mennes, M., Imperati, D., Castellanos, F.X., Sporns, O., Milham, M.P., 2012. Network centrality in the human functional connectome. Cereb. Cortex 22, 1862–1875. http://dx.doi.org/10.1093/cercor/bhr269.