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Elucidating Functional Differences between Cortical Gyri and Sulci via Sparse Representation HCP Grayordinate fMRI Data

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Abstract

The highly convoluted cerebral cortex is characterized by two different topographic structures: convex gyri and concave sulci. Increasing studies have demonstrated that cortical gyri and sulci exhibit different structural connectivity patterns. Inspired by the intrinsic structural differences between gyri and sulci, in this paper, we present a data-driven framework based on sparse representation of fMRI data for functional network inferences, then examine the interactions within and across gyral and sulcal functional networks and finally elucidate possible functional differences using graph theory based properties. We apply the proposed framework to the high-resolution Human Connectome Project (HCP) grayordinate fMRI data. Extensive experimental results on both resting state fMRI data and task-based fMRI data consistently suggested that gyri are more functionally integrated, while sulci are more functionally segregated in the organizational architecture of cerebral cortex, offering novel understanding of the byzantine cerebral cortex.

Keywords

gyri; sulci; sparse representation; functional networks; grayordinate fMRI

1. Introduction

The human cerebral cortex is characterized by the highly convoluted cortical folding patterns, which are composed of convex gyri and concave sulci (Rakic, 1988; Van Essen, 1997). Thanks to recent advances in multimodal neuroimaging techniques, such as high angular resolution diffusion imaging (HARDI) (Tuch et al., 2002) and diffusion tensor imaging (DTI) (Mori and Zhang, 2006), the neuroscientific communities have made remarkable progresses in understanding the underlying structural originations of cerebral cortex via fiber wiring diagrams and functional activities with decent spatial and temporal resolutions. In particular, several inspiring findings from anatomic/structural/functional

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perspectives have been reported that there are intrinsic structural and functional differences of cortical gyri and sulci (Chen et al., 2013; Deng et al., 2014; Fischl and Dale, 2000; Jiang et al., 2015; Nie et al., 2012; Zeng et al., 2015; Zhang et al., 2014). For instance, the cortical thickness on gyri is generally larger than that on sulci in adults (Fischl and Dale, 2000) and in developing infants (Li et al., 2015). In addition, joint analysis of longitudinal structural imaging and DTI revealed that the fiber density on gyral regions was significantly higher than that on sulcal regions in the frontal, temporal, and parietal lobes during neurodevelopment (Li et al., 2015). Besides, previous studies have also shown that cortical gyri and sulci exhibit different structural connectivity patterns (Chen et al., 2013; Nie et al., 2012; Takahashi et al., 2012; Zhang et al., 2014). For example, the axonal fiber terminations were found to dominantly concentrate on gyri, rather than sulci, based on the multimodal representation of cortical gyral folding and streamline fibers (Nie et al., 2012). This finding is replicated in all analyzed cerebrums of human, chimpanzee and macaque (Nie et al., 2012). Similarly, the structural fiber connection patterns closely follow the gyral folding patterns in the tangent direction, and this close relationship is well preserved in the neocortices of macaque, chimpanzee, and human brains, despite of the progressively increasing complexity and variability of cortical folding and structural connection patterns (Chen et al., 2013). Moreover, radial organization from cerebral connectivity of human fetus brain persisted longer in the crests of gyri than at the depths of sulci (Takahashi et al., 2012). Another study verified the presence of these U-shaped streamline fibers in cortical architectures, which is evolutionarily-preserved across primate species and connect neighboring gyri by coursing around cortical sulci (Zhang et al., 2014). In addition, such structural differences between cortical gyri and sulci are more and more prominent during neurodevelopment and in brain evolutions (Chen et al., 2013; Nie et al., 2012; Zhang et al., 2014). These evidences based on structural magnetic resonance imaging consistently suggest a possible structural modulation mechanism that the cortical axogenesis might take effect in cortical folding development. Specifically, the axonal pushing hypothesis of cortical folding has been proposed, which implies that gyri should have a higher density of fiber connection than sulci (Chen et al., 2013; Li et al., 2015; Nie et al., 2012). In parallel with prior findings in macroscale neuroimaging studies in primates, a recent study based on Allen Mouse Brain Connectivity Atlas and the Allen Mouse Brain Atlas found that the cerebellum gyri and sulci of rodent brains are significantly different in both axonal connectivity and gene expression patterns (Zeng et al., 2015).

Inspired by previous anatomical and structural findings and motivated by the fact that DTI-derived the fibers provide the structural substrates for functional activities, recently, more sights have been shifted to explore the differences of functional mechanisms and dynamics between gyri and sulci from a functional perspective (Deng et al., 2014; Jiang et al., 2015; Jiang et al., 2016). For example, Deng and colleagues (Deng et al., 2014) quantitatively characterized the functional model of cortical gyri and sulci of resting-state functional magnetic resonance imaging (rsfMRI) data. Specifically, they first manually labeled a variety of cortical landmarks on the major gyri/sulci of each subject, and then examined the functional connectivities among the labelled gyral and sulcal landmarks in the entire cerebral cortex via rsfMRI data. Their experimental results demonstrated that the functional connectivity is strong between gyral-gyral regions, weak between sulcal-sulcal regions, and

moderate between gyral-sulcal regions. Another intriguing finding is related to task-based heterogeneous functional regions (THFRs) (Jiang et al., 2015) or spatial overlap patterns of functional networks (SOPFNs) (Jiang et al., 2016). Mounting studies in the neuroscience field reported that there exist multiple concurrent functional networks that are spatially distributed across brain regions and interact with each other (Ashburner and Friston, 2000; Bullmore and Sporns, 2009; Fox et al., 2005; Lv et al., 2015a; Lv et al., 2015b). Certain brain regions and networks exhibit strong functional heterogeneity and diversity (Duncan, 2010; Pessoa, 2012). Namely, a brain region might be involved in multiple functional processes simultaneously, and a functional network might recruit heterogeneous brain regions. Interestingly, THFRs activated in multiple tasks conditions were found to locate significantly more on gyral regions than on sulcal regions (Jiang et al., 2015). Furthermore, a study based on a sliding-window method reported that spatial overlap patterns of functional networks also mainly locate on gyral regions across different time periods (Jiang et al., 2016). Taken together, the abovementioned studies consistently suggested a possible, common architecture of cerebral cortex that gyri are global structural and functional centers in the cerebral cortex, while sulci are local structural and functional units.

Although significant achievements have been made for unraveling the relationship mystery between gyri and sulci, there are still some crucial issues to be addressed, to the best of our knowledge. First, the previous study (Deng et al., 2014) assessed the functional model of gyri and sulci based on rsfMRI, putting aside the functional activities in response to task stimulus. Since there exist fundamental intrinsic differences in terms of signal composition patterns of rsfMRI and task-based fMRI (tfMRI) signals (Zhang et al., 2016), it is unclear how the gyri and sulci functionally interact in response to a specific task paradigm. Second, the previous study (Deng et al., 2014) relied on manual labeling of cortical gyral and sulcal landmarks according to the prior knowledge about cerebral cortex. However, the conclusions drawn by this approach might be incomplete, since a slightly displaced landmark could have quite different structural or functional connectivity profiles (Li et al., 2009; Zhu et al., 2012a). Therefore, it is more desired to use data-driven models, such as independent component analysis (ICA) (Calhoun et al., 2009) and sparse representation (Mairal et al., 2010), to investigate the functional characteristics of human brain. Especially, sparse representation has been successfully applied in human brain mapping field to represent brain functional activities compactly and to detect meaningful functional networks effectively (Abolghasemi et al., 2015; Lee et al., 2011; Lv et al., 2015a; Lv et al., 2015b). Third, the functional integration and segregation of gyral and sulcal connectivities are largely unknown, which can be characterized and assessed by graph theory based properties (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010). The significant differences of these graph-based properties could reflect that gyri and sulci may play different roles in the functional organization of the cortical architecture.

To address abovementioned problems, in this paper, we present a data-driven framework based on sparse representation of fMRI data to elucidate the functional differences between cortical gyri and sulci. The motivation of sparse representation for this work is due to three advantages of using sparse representation. First, sparse representation is a purely data-driven model and will not introduce subjective bias (Mairal et al., 2010), and thus the potential conclusions drawn from sparse representation would be complementary to the findings in

previous study in which the functional connectivity was estimated among manually labelled landmarks (Deng et al., 2014). Second, mounting neuroscientific studies have supported that sparse population coding of a set of neurons seems more effective than independent exploration (Daubechies et al., 2009). Therefore, it is well-justified to explore neural activities using sparse representation. Third, the sparse coding has been proven to be efficient and effective for functional network inference from fMRI data (Lv et al., 2015a; Lv et al., 2015b). We adopt high-resolution rsfMRI and tfMRI signals from the recently publicly released Human Connectome Project (HCP) grayordinate datasets (Barch et al., 2013; Glasser et al., 2013; Smith et al., 2013; Van Essen et al., 2013), given that the grayordinate datasets offer precise group-wise spatial correspondence across a large population and can differentiate gyral/sulcal regions sufficiently (Glasser et al., 2013). Specifically, fMRI signals on cortical gyri or sulci are extracted separately for all individuals. Following this, the collections of gyral or sulcal fMRI signals are sparsely represented via the online dictionary learning and sparse representation algorithm (Lv et al., 2015a; Mairal et al., 2010) for functional network inferences. Notably, the gyral and sulcal fMRI signals can be compactly and sparsely represented by an atomic dictionary, in which each atom corresponds to a representative fMRI signal pattern (Lv et al., 2015a). Afterwards, the interactions within and across gyral and sulcal functional networks are were estimated from the learned gyral and sulcal dictionary matrices and then quantitatively examined to reveal possible functional differences between gyri and sulci. What's more, to further understand the functional segregation and integration of cerebral cortex, graph theory-based properties (Bullmore and Sporns, 2009) of gyral and sulcal functional connectivities are also investigated, including average clustering coefficient (Watts and Strogatz, 1998), modularity (Newman, 2006) and global efficiency (Latora and Marchiori, 2001). Our experimental results demonstrated that resting state networks and task-evoked networks can be effectively and reliably identified by sparse representation of the grayordinate fMRI data. Extensive experimental results on both rsfMRI data and tfMRI data consistently suggested that gyri are more functionally integrated, while sulci are more functionally segregated in the functional architecture of cerebral cortex, which offers novel understanding of the byzantine cerebral cortex.

2. Results

We performed a series of experiments to elucidate the functional differences of cortical gyri and sulci. These experimental results are detailed in the followings subsections of “Parameter setting of sparse representation”, “Group-wise consistent components of gyri and sulci”, “Distribution differences between gyral and sulcal functional connectivities”, and “Graph theory based differences gyral and sulcal functional connectivities”, respectively.

2.1. Parameter setting of sparse representation

Optimal parameter setting of sparse representation is still an open question in the machine learning field. Given the lack of golden standard in determining optimal parameters of sparse representation, to evaluate the impact of parameter setting, we tried multiple combinations of different dictionary sizes and different regularization coefficients using grid research. Specifically, the dictionary size k was set from 200 to 400 with an interval of 100,

while the regularization coefficient λ was set from 0.05 to 0.15 with an interval of 0.05. In total, nine parameter combinations were tested in our work. Given that the grid search procedure is time consuming, in this paper, we randomly chose fMRI data of 10 subjects from HCP motor task to assess the validity of our findings. Interestingly, the graph theory-based differences between sulci and gyri illustrated in this paper were consistently replicated with different parameter combinations (details in Table 1), indicating the robustness and validity of our findings. Specifically, average cluster coefficient and global efficiency of gyral functional connectivity matrices are statistically higher than that of sulcal ones, whereas sulcal functional connectivity matrices have higher modularity than gyral ones, suggesting that gyri are functionally integrated while sulci are functionally segregated. Given the reproducibility of our results enabled by the grid search procedure, in the following sections, these experimental results were generated based on the setting of dictionary size $k = 200$ and regularization parameter $\lambda = 0.1$ for the HCP grayordinate fMRI data.

2.2. Group-wise consistent components of gyri and sulci

In this section, we evaluate the effectiveness of sparse representation using group-wise clustering for rsfMRI data and temporal frequency analysis for tfMRI data, respectively. Regarding group-wise spatial correspondences in the grayordinate fMRI data, the gyral and sulcal functional networks of all subjects can be mapped back to the standard cortex template, although dictionary learning method is applied to the fMRI data in an individual way. Specifically, we employ the k-means clustering algorithm to infer the group-wise consistent spatial patterns from gyral or sulcal spatial patterns. The representative group-wise consistent gyral and sulcal components identified by the clustering procedure are visualized in Fig. 1. Note that these visualized spatial patterns can be consistently found in all subjects. In addition, every spatial pattern has its neuroscientific interpretation. For example, these gyral clusters on the top row are known as the well-established resting-state networks (Smith et al., 2009), including posterior part of default mode network (Fig. 1a) (Raichle et al., 2001), the fronto-parietal networks in both hemisphere (Fig. 1b and Fig. 1c) and occipital gyrus (Fig. 1d). Meanwhile, the sulcal clusters in the bottom row represent precuneus (Fig. 1e), intraparietal sulcus (Fig. 1f), premotor cortex (Fig. 1g) and calcarine sulcus (Fig. 1h), respectively. In comparison with gyral components, it seems that the sulcal components are more isolated. The clustering results confirm that the dictionary learning and sparse representation algorithm reliably uncover meaningful brain networks from the grayordinate fMRI data. In addition, the results qualitatively suggest that gyri are more functionally integrated among remote brain regions.

In terms of task-based fMRI data, the most prominent and intuitive functional components obtained by sparse representation are the task-evoked networks which can be identified by temporal frequency analysis in (Lv et al., 2015a). Specifically, the time series of a task-evoked component and its spatial characteristics were compared with those of task paradigm curves. Moreover, the frequency characteristics of these gyral and sulcal components were examined using fast Fourier analysis. For instance, there are exemplar gyral and sulcal components related to visual cue in the motor task as shown in Fig. 2. Generally, the spatial distributions of the two components are very similar to the results from the corresponding group-wise general linear model (GLM) derived activation map. In addition, their time

courses, as shown in Fig. 2c and 2d, are also highly correlated with the corresponding task design contrast curves with correlation of 0.846 and 0.832. Furthermore, the frequency spectrum of its time series (Fig. 2e and 2f) is highly concentrated on the task design frequency. Given the characteristics in spatial/temporal/frequency domain, we can confirm that that sparse representation could also identify task-evoked functional components in the individual fMRI data. Taken together, the sparse representation of whole-brain fMRI data can identify both resting-state networks and task-evoked networks efficiently and reliably.

2.3. Distributions of functional connectivities among gyral and sulcal components

In this section, we analyze the distributions of functional connectivity strength among gyral and sulcal components in the whole cerebral cortex. Specifically, the functional connectivity was estimated between any pair of gyrus/gyrus, gyrus/sulcus, and sulcus/sulcus network component combinations. We examine the distribution differences by thresholding the absolute correlation matrices to maintain the top 5% of the highest connections. The functional connectivity matrices and their detailed distribution histograms of three combination types (gyrus/gyrus, gyrus/sulcus, and sulcus/sulcus pairs) are shown for resting-state fMRI data (Fig. 3a) and seven task-based fMRI datasets (Fig. 3b–h). As can be seen from the Fig. 3 that the gyri-gyri functional connectivities have the highest probability of larger connectivity magnitude for all levels in the histogram. In contrast, sulci-sulci functional connectivities have the lowest probability of larger connectivity magnitude in the histogram. Meanwhile, the probability of gyri-sulci connectivity is in-between. Note that this finding is replicated both in resting-state fMRI and all seven task-based fMRI datasets. The above findings suggest that gyri, rather than sulci, are global functional connection centers, whenever the brain are under resting-state state or in response to different task paradigms, which further replicates and supports our prior functional model of cortical gyri and sulci that gyri are the global functional core, while sulci are the local functional units (Deng et al., 2014).

We further quantitatively summarized the distribution differences among the three types of distributions. The distribution differences are shown in Fig. 4 for both rsfMRI and tfMRI data. On average, the survived connectivities among gyral-gyri, gyri-sulci and sulci-sulci connection patterns account for a rate of 41.2%, 36.4% and 22.4%, respectively. These results suggest that majority of the strong functional connections to gyral regions is originated from gyri too, which further lend supports to our prior functional model of cortical gyri and sulci that gyri are functional connection centers (Deng et al., 2014).

2.4. Graph theory based differences between gyral and sulcal connectivity

The graph theory-based differences between gyral and sulcal functional connectivity are shown in Fig. 5. It is evident that gyri-gyri connectivity has higher value for average cluster coefficient, which is reproducible for all the resting-state and seven task-based fMRI datasets that we analyzed, suggesting that gyri are more locally efficient than sulci (Watts and Strogatz, 1998). Additionally, the gyri-gyri connectivities have higher global efficiency than sulci-sulci connectivities. These differences have been validated by right-tail pair-wise t-test ($p < 0.001$). These results consistently indicate that gyral functional connectivity has significantly higher global and local efficiency of parallel information transfer and higher

local fault tolerance for low connection density (Watts and Strogatz, 1998). In other words, gyral regions is favorable to facilitate the information flows in remote cortical areas. In contrast, sulci regions have lower global and local efficiency properties, so they might be responsible for local information processing. The third property is modularity that depicts the functional segregation and integration of human brain (Sporns and Betzel, 2016). The modularity of sulcal connectivity is higher when the subjects are in response to task paradigms, which suggests that the sulcal regions is more partitioned as independent modules and more locally organized (Bullmore and Sporns, 2009). Notably, the modularity exhibits no significant difference between gyral and sulcal connectivity in resting-state fMRI data. This phenomenon might arise from that functional modules can fluctuate in relation to cognitive states (Sporns and Betzel, 2016). That is, the sulcal regions become increasingly more modular (i.e., more segregated) during task performances, while gyri become increasingly less modular (i.e., more integrated). This finding further demonstrates that gyri are responsible for global information exchange in the cerebral cortex. Overall, these results based on graph theory offer additional strong support to existing perspectives reported in the previous studies (Chen et al., 2013; Deng et al., 2014; Jiang et al., 2015; Nie et al., 2012).

3. Conclusions and Discussion

In this paper, we were motivated to elucidate functional differences of cortical gyri and sulci. Specifically, we presented a data-driven framework based on sparse representation of grayordinate fMRI data for functional network inferences, examined the interactions within and across gyral and sulcal functional networks, and finally assessed the distribution and graph theory-based differences of these functional connectivity matrices. The grayordinate fMRI data of all subjects in HCP Q1 datasets were used to examine the above hypothesized functional working mechanisms of the human brain. Interestingly, we found that the interactions among gyri are strong, whereas the interactions among sulci are weak. In addition, gyral connectivity matrices have higher average cluster coefficient and higher global efficiency than sulcal ones, indicating a common principle of human cerebral cortex that gyri are favorable to facilitate the information flows in remote cortical areas while sulci might be responsible for local information processing. Notably, these results are replicated in both resting-state fMRI and seven task-based fMRI. Furthermore, in response to task stimulus, the sulci become increasingly more modular (i.e., more segregated), while gyri become increasingly less modular (i.e., more integrated). In general, our experimental results based on the HCP grayordinate data consistently suggested that gyri are more functionally integrated, while sulci are more functionally segregated in the organizational architecture of cerebral cortex, which offers a better understanding of the byzantine cerebral cortex. The verified functional model and its associated computational approaches could potentially facilitate many novel applications in neuroimaging, cognitive neuroscience and clinical neuroscience. For instance, the differentiation of the functional roles of gyri and sulci might help achieve better localization and selection of brain regions in different functional neuroimaging and cognitive neuroscience studies.

In the future, the proposed framework in this study can be extended in the following directions. First, it is desired to use parameter optimization methods, such as minimum description length criterion (Lee et al., 2011; Rissanen, 1978) to determine the optimal

parameters in sparse representation. One of the limitations in our experiments is that the parameters in sparse representation, e.g., regularization parameters and dictionary size, were set based on our empirical experience, though we have already tried different combinations of these parameters. Though functional networks is quite monotonous with the setting of lambda and the interested components can be stably reconstructed when the dictionary size is in a certain range (Lv et al., 2015a), it is still necessary to perform reproducibility studies and theoretical examinations with regard to different parameter settings.

Second, the functional connectivities among gyral–gyral and sulcal–sulcal network components can be used to elucidate the potential dysfunctions in many neurological or psychiatric diseases, such as schizophrenia (Menon, 2011). Furthermore, several recent studies demonstrated the existence of temporal dynamics of functional connectivity in fMRI datasets (Allen et al., 2014; Bassett et al., 2011; Chang and Glover, 2010; Deco and Jirsa, 2012; Latora and Marchiori, 2001; Majeed et al., 2011). For instance, a recent study (Latora and Marchiori, 2001) demonstrated the association between the resting-state connectivity variations and the intrinsic activities of specific networks, which can provide insights on the dynamic changes in large-scale brain connectivity and network configurations. Therefore, improved measurements of functional connectivity that can account for temporal dynamics should be explored in the future to examine the temporal dynamics of functional connectivity models of cortical gyri and sulci presented in this work.

4. Experimental Procedure

4.1. Grayordinate fMRI Data Acquisition and Preprocessing

Both rsfMRI and tfMRI signals from the high-resolution HCP Q1 grayordinate data (Barch et al., 2013; Glasser et al., 2013; Smith et al., 2013; Van Essen et al., 2013) were adopted in this study. Specifically, the tfMRI data are designed to identify core functional nodes across a wide range of cerebral cortex (Barch et al., 2013). The tfMRI data, consist of seven task paradigms, including emotion, gambling, language, motor, relational, social, and working memory. The detailed designs of the seven task paradigms are referred to (Barch et al., 2013).

In total, there are 68 subjects in the HCP Q1 release (Barch et al., 2013; Van Essen et al., 2013). The acquisition parameters of HCP data are as follows: 90×104 matrix, 220 mm FOV, 72 slices, TR = 0.72 s, TE = 33.1 ms, flip angle 52°, BW = 2,290 Hz/Px, in-plane FOV = 208×180 mm and 2.0 mm isotropic voxels. The HCP grayordinate fMRI data was preprocessed by the minimal preprocessing pipelines (Glasser et al., 2013), mainly including spatial artifacts and distortions removal, cortical surfaces generation, within-subject cross-modal registration, cross-subject registration to standard volume and surface spaces, and generation of a CIFTI format of preprocessed data in the standard grayordinate space (Glasser et al., 2013). In brief, gray matter is modeled as combined cortical surface vertices and subcortical voxels, and the term “grayordinates” is adopted to describe the spatial dimension of such combined coordinate system. There are 91,282 aligned grayordinates, including about 60,000 gray matter vertices on the standard cortical surface and about 30,000 vertices in subcortical regions (Glasser et al., 2013). The grayordinate fMRI data is represented as a 2D matrix, in which one dimension represents the standard grayordinates

(spatial information) which have correspondence across subjects and the other dimension represents the fMRI time series (Barch et al., 2013; Glasser et al., 2013; Van Essen et al., 2013).

4.2. Overview

The proposed framework is summarized in Fig. 6. First, we divided the whole-brain fMRI data from each subject (Fig. 6a) into gyral fMRI data and sulcal fMRI data (Fig. 6b) under the structural information of sulcal depth value. Then, the online dictionary learning and sparse representation algorithm (Mairal et al., 2010) was applied to the gyral and sulcal fMRI data, respectively. Notably, the sparse representation algorithm factorizes the fMRI data into an atomic dictionary matrix (e.g. time courses, Fig. 6c) and a sparse reference weight matrix (e.g., spatial maps, Fig. 6d). Here, each atom in the dictionary matrix corresponds to a representative fMRI signal pattern while the corresponding row of the weight matrix stores the information of the spatial distributions (Lv et al., 2015a). In order to validate the effectiveness of sparse representation, we inferred group-wise consistent brain networks from the reference weight matrix using the classical k-means clustering algorithm (Fig. 6g) and the temporal-frequency analysis proposed in (Lv et al., 2015a). Afterwards, we estimated the functional connectivity matrix (Fig. 6e) by Pearson correlation coefficient between the atoms of the learned gyral and sulcal dictionary matrices. Finally, the distributions and graph theory based properties of gyral and sulcal functional connectivity networks were quantitatively characterized and assessed (Fig. 6f).

4.3. Sparse representation of fMRI data

We learned temporal dictionary components and functional networks from grayordinate fMRI data for each subject via our recently developed computational framework (Lv et al., 2015a; Lv et al., 2015b). First, we separated gyral and sulcal fMRI signals from whole-brain grayordinate fMRI data according to the structural information of sulcal depth. After normalizing to zero mean and unit norm, the gyral and sulcal fMRI signals were aggregated into a 2D signal matrix $\mathbf{X} = [\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n] \in \mathbb{R}^{t \times n}$, where t is the number of time points and n is the number of gyral or sulcal grayordinates. Then $\mathbf{X}$ was factorized into an atomic dictionary basis matrix $\mathbf{D} = [\mathbf{d}_1, \mathbf{d}_2, \dots, \mathbf{d}_k] \in \mathbb{R}^{t \times k}$ (is the dictionary component size) and a sparse reference weight matrix $\mathbf{a} = [\mathbf{a}_1, \mathbf{a}_2, \dots, \mathbf{a}_n] \in \mathbb{R}^{k \times n}$. Formally, the empirical cost function $\mathcal{L}(\mathbf{x}, \mathbf{D})$ in online dictionary learning takes the average regression loss of all n fMRI signals into consideration, as formulated in Eq. (1).

$$f_n(\mathbf{D}) \triangleq \frac{1}{n} \sum_{i=1}^n \ell(\mathbf{x}_i, \mathbf{D}) = \frac{1}{n} \sum_{i=1}^n \min_{\alpha_i \in \mathbb{R}^k} \frac{1}{2} \|\mathbf{x}_i - \mathbf{D}\alpha_i\|_2^2 + \lambda \|\alpha_i\|_1 \quad (1)$$

where the cost function $\mathcal{L}(\mathbf{x}, \mathbf{D})$ is defined as the optimal value of sparse representation:

$\ell(\mathbf{x}, \mathbf{D}) = \min_{\alpha \in \mathbb{R}^k} \frac{1}{2} \|\mathbf{x} - \mathbf{D}\alpha\|_2^2 + \lambda \|\alpha\|_1$. Note that the value of $\mathcal{L}(\mathbf{x}, \mathbf{D})$ should be small if signal $\mathbf{x}$ is reasonably well represented by $\mathbf{D}$. The first term considers the signal reconstruction residuals while the second term accounts for ℓ_1 sparsity regularizations which

yields sparse solutions of weight matrix. λ is a regularization parameter that trades off regression residuals and sparsity levels.

To prevent $\mathbf{D}$ from being arbitrarily large, the columns in $\mathbf{D}$ are constrained by Eq. (2). Eventually, the problem of minimizing Eq. (1) can be rewritten as a matrix factorization problem with a sparsity penalty in Eq. (3).

$$\mathbf{C} \triangleq \left\{ \mathbf{D} \in \mathbb{R}^{t \times k} \text{ s.t. } \forall j=1, \dots, m, d_j^T d_j \leq 1 \right\} \quad (2)$$

$$\min_{\mathbf{D} \in \mathbf{C}, \boldsymbol{\alpha} \in \mathbb{R}^{k \times n}} \frac{1}{2} \|\mathbf{X} - \mathbf{D}\boldsymbol{\alpha}\|_F^2 + \lambda \|\boldsymbol{\alpha}\|_{1,1} \quad (3)$$

We adopted the effective online dictionary learning algorithm and the associated publicly released online dictionary learning toolbox (Mairal et al., 2010) to solve Eq. (3). The online dictionary learning algorithm is based on stochastic approximations and the least angle regression (LARS)-Lasso algorithm (Mairal et al., 2010). In brief, it processes one sample at a time, and uses second-order information of the cost function to efficiently solve the dictionary learning by sequentially minimizing a quadratic local surrogate of the expected cost. The dictionary learning algorithm consists of a sequence of iterative updates of $\mathbf{D}$. In each iteration, it draws one training sample at a time, and alternates classical sparse coding steps for computing the decomposition $\boldsymbol{\alpha}_t$ of $\mathbf{X}_t$ over the dictionary $\mathbf{D}_{t-1}$ obtained at the previous iteration, with dictionary update steps where the new dictionary $\mathbf{D}_t$ is computed by minimizing over the cost function. The updating of the dictionary is based on block-coordinate descent with warm restarts, which is parameter free and does not require any learning rate tuning (Mairal et al., 2010). It has been proven that the iterations of dictionary update can achieve convergence to learn an optimal $\mathbf{D}$. Once $\mathbf{D}$ is learned and fixed in Eq. (3), the sparse representation based on the learned $\mathbf{D}$ can be solved as an ℓ_1 -regularized linear least squares problem to learn an optimized $\boldsymbol{\alpha}$ (Mairal et al., 2010). After dictionary learning and sparse representation, the fMRI signal matrix can be represented by a learned dictionary matrix $\mathbf{D}$ and a sparse reference weight matrix $\boldsymbol{\alpha}$. Notably, each column in the dictionary matrix corresponds to a representative fMRI time series pattern, whereas each row in the reference weight matrix represent the spatial distribution of corresponding component for the reconstruction of the fMRI signal (Lv et al., 2015a). Given the inter-subject structural variability of cerebral cortex, the dictionary learning algorithm was applied to the whole-brain fMRI data on cortical gyri and sulci of each individual subject.

4.4. Functional connectivity estimation

As noted above, the columns in the atomic dictionary matrix indicate representative fMRI signal patterns (e.g. time course) of a component and the corresponding rows in the reference matrix represents the spatial distribution (e.g. spatial maps) of the corresponding component (Lv et al., 2015a). There are no inter-subject correspondences of the learned temporal or spatial components, since the online dictionary learning algorithm was applied

to the fMRI data of individual subject. Therefore, the comparison of functional characteristics of gyral and sulcal functional connectivities across different brains are established at the gyri/sulci level. Specifically, for a pair of the gyral or sulcal components, the functional connectivity was computed by the Pearson correlation coefficient between their temporal patterns (Deng et al., 2014; Zhu et al., 2012b). Given that the distributions of functional connectivity values could vary across different subjects, the mean functional correlation value and the standard deviation per subject were used to normalize the corresponding subject's functional connectivity correlation matrix as in Eq. (4) (Deng et al., 2014).

$$FC(X, Y) = \frac{FC(X, Y) - \mu}{4\sigma} \quad (4)$$

where μ is the average FC of the corresponding subject; σ is the standard deviation; 4σ , as commonly used in statistics, is considered as a cut-off threshold of the Gaussian distribution. After normalization, the average level of a functional connection matrix would have a value of 0. Henceforth, this normalization procedure provides more consistent and comparable individual distributions and enables fair comparisons of functional connectivity across different subjects (Deng et al., 2014). Intuitively, the larger the absolute connectivity value is, the stronger the functional connectivity will be.

4.5. Graph theory based properties

We hypothesized that gyral and sulcal functional connectivity might exhibit different graph theory based properties. To examine this hypothesis, we evaluated three graph theory-based properties related to network efficiency and modularity (Bullmore and Sporns, 2009), and further examined whether there exist significant difference among these graph theory based properties among the gyri/sulci functional connectivity networks. Specifically, these graph theory based properties included average clustering coefficients (Bullmore and Sporns, 2009), global efficiency (Watts and Strogatz, 1998) and modularity (Newman, 2006). The average clustering coefficient measures the efficiency of the local information transmission of each node (Watts and Strogatz, 1998), whereas the global efficiency measures the information transmission efficiency of the entire network (Latora and Marchiori, 2001). In addition, modularity estimates the extent the whole network is segregated into sub-communities (Newman, 2006). In this study, graph properties were estimated from binary unidirectional networks using the brain connectivity toolbox (Rubinov and Sporns, 2010). Specifically, binary unidirectional functional connectivities were built by thresholding the absolute functional connectivity matrices to maintain the top 5% of the strongest connections for gyri and sulci. The statically significant differences between graph properties of gyri/sulci functional connectivities were compared using pair-wise *t* test.

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Highlights

1. A new sparse representation framework to elucidate functional differences between gyri and sulci.
2. Results suggested that gyri are more functionally integrated.
3. Results suggested that sulci are more functionally segregated.
4. Offering novel understanding of the byzantine cerebral cortex.

Fig. 1.

The group-wise consistent functional networks derived by sparse representation in grayordinate fMRI data. (a–d): Gyral spatial components, including the posterior part of default mode network (a), left fronto-parietal attention network (b), right fronto-parietal network (c), and occipital visual cortex (d). (e–h): Sulcal spatial components, including precuneus (e), intraparietal sulcus (f), premotor cortex (g) and calcarine sulcus (h).

Fig. 2.

Exemplar task-evoked common functional components from the visual cue design in motor task fMRI data. (a–b): Group-wise spatial patterns of gyri and sulci in tfMRI data that are mapped on the cortical surface; (c–d): Time series of these components (blue), task design contrast curves of motor task (orange); (e–f): frequency spectrum of the components (blue) and the contrast curve (orange).

Fig. 3. The functional connectivity matrices among gyral/sulcal components and their histograms in HCP grayordinate rsfMRI and seven tfMRI datasets. (a) Resting-state fMRI. (b–h): Results for emotion, gambling, language, motor, relational, social and working memory tfMRI data, respectively.

Fig. 4.

The portions of each kind of functional connectivities in the top 5% highest functional connectivity strength. Notably, the gyri-gyri connectivity patterns account for the largest share, while the sulci-sulci connectivity patterns account for the least share for both rsfMRI and tfMRI data.

Fig. 5. Graph theory-based differences between gyral and sulcal functional connectivities, including average cluster coefficients (top panel), global efficiency (middle panel) and modularity (bottom panel).

Fig. 6. The system overview of the proposed framework. (a) Whole-brain grayordinate fMRI data. (b) Gyral and sulcal fMRI data. (c) Dictionary matrix. (d) Reference weight matrix. Red color indicates gyral components while blue color represents sulcal components. (e) Gyral-gyral, gyral-sulcal and sulcal-sulcal functional connectivity matrices. (f) Graph theory based differences. (g) Group-wise consistent brain networks.

Table 1

The graph metrics of gyral and sulcal functional connectivity with different parameter combinations of sparse representation . ACC, GE and MODU denote average cluster coefficient, global efficiency and modularity, respectively.

Parameter		ACC		GE		MODU	
		Gyri	Sulci	Gyri	Sulci	Gyri	Sulci
k	λ						
200	0.05	0.31±0.05	0.25±0.04	0.34±0.04	0.20±0.03	0.26±0.02	0.31±0.06
200	0.10	0.35±0.06	0.31±0.04	0.36±0.04	0.22±0.03	0.26±0.01	0.31±0.06
200	0.15	0.36±0.06	0.30±0.04	0.34±0.05	0.19±0.02	0.25±0.02	0.30±0.06
300	0.05	0.33±0.04	0.29±0.05	0.37±0.05	0.24±0.03	0.23±0.02	0.27±0.04
300	0.10	0.38±0.05	0.34±0.03	0.39±0.05	0.25±0.03	0.24±0.02	0.28±0.04
300	0.15	0.40±0.06	0.35±0.02	0.38±0.04	0.22±0.03	0.24±0.02	0.27±0.05
400	0.05	0.36±0.05	0.30±0.06	0.40±0.04	0.28±0.03	0.22±0.02	0.26±0.04
400	0.10	0.40±0.05	0.37±0.03	0.41±0.04	0.27±0.03	0.23±0.02	0.27±0.04
400	0.15	0.42±0.05	0.38±0.04	0.40±0.05	0.25±0.03	0.22±0.02	0.27±0.04