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Age-related decrease in functional connectivity of the right fronto-insular cortex with the central executive and default-mode networks in adults from young to middle age

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HIGHLIGHTS

- We found age-related decreases in the positive FCs between the rFIC and the CEN.
- We found age-related decreases in the negative FCs between the rFIC and the DMN.
- The disconnection may influence the switching role of the rFIC between CEN and DMN.

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ABSTRACT

The right fronto-insular cortex (rFIC) is a core node of the salience network (SN) and plays a critical role in switching between the central executive network (CEN) and the default-mode network (DMN), an important function in cognitive processing. In the present study, we tested the hypothesis that the functional connectivity (FC) between the rFIC and the CEN and DMN may decrease with age in adults from youth to middle age given that the intra- and inter-network FCs of the three networks decline in aged people. We performed voxel-wise FC analysis based on resting state functional MRI data (171 subjects; 17–62 years of age) to investigate whether the FCs of the rFIC are associated with age in normal adults. We found age-related decreases in the positive FCs between the rFIC and the CEN and in the negative FCs between the rFIC and the DMN with and without atrophy correction. These findings suggest that the connection of the rFIC with the CEN and DMN is degraded even in middle-aged adults, which may influence the role of the rFIC in effectively switching between the CEN and DMN and may further affect cognitive function in these subjects.

1. Introduction

The right fronto-insular cortex (rFIC) is the core node of the salience network (SN) that serves to identify salient stimuli to guide behavior [19,25]. The rFIC has been reported to play a critical role in switching between the central executive network (CEN) and the default-mode network (DMN) [26]. The CEN mainly includes the dorsolateral prefrontal cortex (DLPFC) and the posterior parietal cortex (PPC); the DMN includes the medial prefrontal cortex and anterior cingulate cortex (MPFC/ACC), the posterior cingulate cortex and precuneus (PCC/Pcu), the lateral parietal regions, and (likely) the medial temporal lobes; and the SN consists of the ventrolateral prefrontal cortex (VLPFC), FIC, and ACC [3,10,11,25]. During the performance of cognitively demanding tasks, the CEN and SN typically show increases in activation, whereas the DMN shows decreases in activation [24,25]. Once a salient stimulus is detected, the rFIC initiates the appropriate transient control signals to engage the CEN in mediating attention, working memory, and other higher order cognitive processes while disengaging the DMN via the large axons of the von Economo neurons (VENs) [1,19]. Importantly, the switching mechanism helps to focus attention on external stimuli. As a result, those stimuli take on added significance or saliency.

Recently, several studies have reported that both the intra-network functional connectivities (FCs) in the DMN [7], SN [21],

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and CEN [20], and their inter-network connectivity [21,27] changed with age. A pioneer study has reported that the inter-network FCs decreased with aging in 73 subjects with ages ranging from 36 to 86 years [21]. Because the SN, CEN, and DMN interact so closely to control cognitive processes, and each has been shown to be related to aging, we hypothesized that the "switching" function of the rFIC between the CEN and the DMN may be impaired even in middle-aged subjects. To validate the hypothesis, we investigated the correlations between age and the FCs of the rFIC based on resting-state functional MRI (fMRI) data. We predicted that the positive FCs between the rFIC and the CEN and the negative FCs between the rFIC and the DMN are both gradually decreased with age in adults from youth to middle age.

2. Materials and methods

2.1. Subjects

This study was approved by the Medical Research Ethics Committee of Xuanwu Hospital of Capital Medical University, and written informed consent was obtained from all participants. This study included 192 normal individuals ranging in age from 17 to 62 years old. All participants were right-handed and had no history of neurological or psychiatric disorders. None of the subjects had visible abnormalities on conventional MR images, including apparent brain atrophy, silent brain infarction or pathological subcortical white matter lesions. Twenty-one subjects were excluded due to excessive head motion during fMRI scanning. In total, 171 subjects (107 men, 64 women) were included in the analyses (Table S1).

2.2. Image acquisition

MR images were acquired on a 3.0 T MR scanner (Magnetom Trio, Siemens, Germany). Resting-state fMRI scans were acquired with an echo planar imaging (EPI) sequence with the following scan parameters: repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle (FA) = 90°, matrix = 64 × 64, field of view (FOV) = 220 mm × 220 mm, slice thickness = 3 mm, and slice gap = 1 mm. Each brain volume comprised 32 axial slices, and 180 volumes were acquired. During fMRI scans, all subjects were instructed to keep their eyes closed, to stay as motionless as possible, to think of nothing in particular, and to not fall asleep. Sagittal T1-weighted MR images were acquired by a magnetization prepared rapid acquisition gradient echo sequence (TR/TE = 2000/2.6 ms; FA = 9°; matrix = 256 × 224; FOV = 256 mm × 224 mm; inversion time = 900 ms; slice thickness = 1 mm, no gap; 176 slices).

2.3. Preprocessing of structural MRI data

Structural MRI data were preprocessed using Statistical Parametric Mapping software (SPM8; http://www.fil.ion.ucl.ac.uk/spm/software/spm8). The structural MR images were segmented into gray matter (GM), white matter and cerebrospinal fluid. After an initial affine registration of the GM concentration map into Montreal Neurological Institute (MNI) space, the GM images were non-linearly warped using diffeomorphic anatomical registration using the exponentiated Lie algebra (DARTEL) technique and were resliced to a resolution of 1.5 mm × 1.5 mm × 1.5 mm. The GMV of each voxel was obtained by multiplying the GM concentration map by the non-linear determinants derived from the non-linear normalization step. Finally, to compensate for residual between-subject anatomical differences, the GMV images were smoothed with a full-width at half-maximum (FWHM) kernel of 8 mm. In effect, the GMV represents the probability that each voxel is gray matter with a correction for individual brain sizes. After spatial preprocessing, the smoothed, normalized GMV maps were used for statistical analysis.

2.4. Preprocessing of resting-state fMRI data

Functional MRI data were analyzed using the Data Processing Assistant for Resting-State fMRI (DPARSFA)[30]. The first 10 volumes from each subject were discarded to allow the signal to reach equilibrium and to allow the participants to adapt to the scanning noise. The remaining 170 volumes were corrected for acquisition time delay between slices. Head motion parameters were then estimated, and each volume was realigned to the mean map of the whole volumes to correct for geometric displacements using a six-parameter rigid-body transformation. Twenty-one subjects were excluded from further analysis because they had maximum displacements in one or more of the orthogonal directions (x, y, z) of >1 mm or a maximum rotation (x, y, z) > 1.0°. The data were spatially normalized to the standard EPI template and resampled to 3 mm × 3 mm × 3 mm. The normalized data were smoothed using a 6 mm FWHM. Several sources of spurious variances, including the estimated motion parameters, linear drift, global average BOLD signals, and average BOLD signals in ventricular and white matter regions, were removed from the data through linear regression. Finally, temporal band-pass filtering (0.01–0.08 Hz) was performed on the time series of each voxel to reduce the effects of low-frequency drift and high-frequency noise.

2.5. FC analyses of the rFIC

The seed region of interest (ROI) of the rFIC was defined as a set of voxels contained in 10-mm sphere centered at the peak of activation cluster (MNI coordinates: 37, 25, −4) obtained from a former study focused on the role of the rFIC [26]. The seed ROI was used throughout the subsequent analyses. The mean time course of the seed ROI was extracted by averaging the time series of the voxels contained in the ROI. Pearson correlation coefficients between the mean time series of the seed ROI and that of each voxel of the whole brain were computed and converted to z values using Fisher's r-to-z transformation to improve the normality. Then, individuals' z-values were entered into a random effect one-sample t test in a voxel-wise manner to identify brain regions that showed significant positive or negative correlations with the seed ROI. A family-wise error (FWE) method with a threshold of $P < 0.05$ was used to correct for multiple comparisons within the gray matter mask of the whole brain except for the cerebellum. Finally, positive and negative FC maps were extracted as the masks for the subsequent correlation analysis.

2.6. Correlations between age and FCs of the rFIC

Considering the non-normal distribution of ages, a non-parametric voxel-based correlation analysis (controlling for gender) between age and FCs of the rFIC were performed within the positive and negative FC masks of the seed ROI, respectively. The non-parametric inference (10,000 permutations) was based on the framework of the general linear model (GLM) in FSL software (http://fsl.fmrib.ox.ac.uk/fsl/). Multiple comparisons were corrected using the FWE method ($P < 0.05$) within the positive or negative FC mask. To further validate correlations between age and the FCs of the rFIC with representative regions of the SN, CEN, and DMN, we extracted significant brain regions within the SN, CEN, and DMN as target ROIs. Each of these target ROIs included 50 voxels centered at its peak coordinate. Then, the mean FC between the seed ROI and the target ROI was computed, and the Spearman correlation coefficient (rs) between each FC and age was tested after regressing

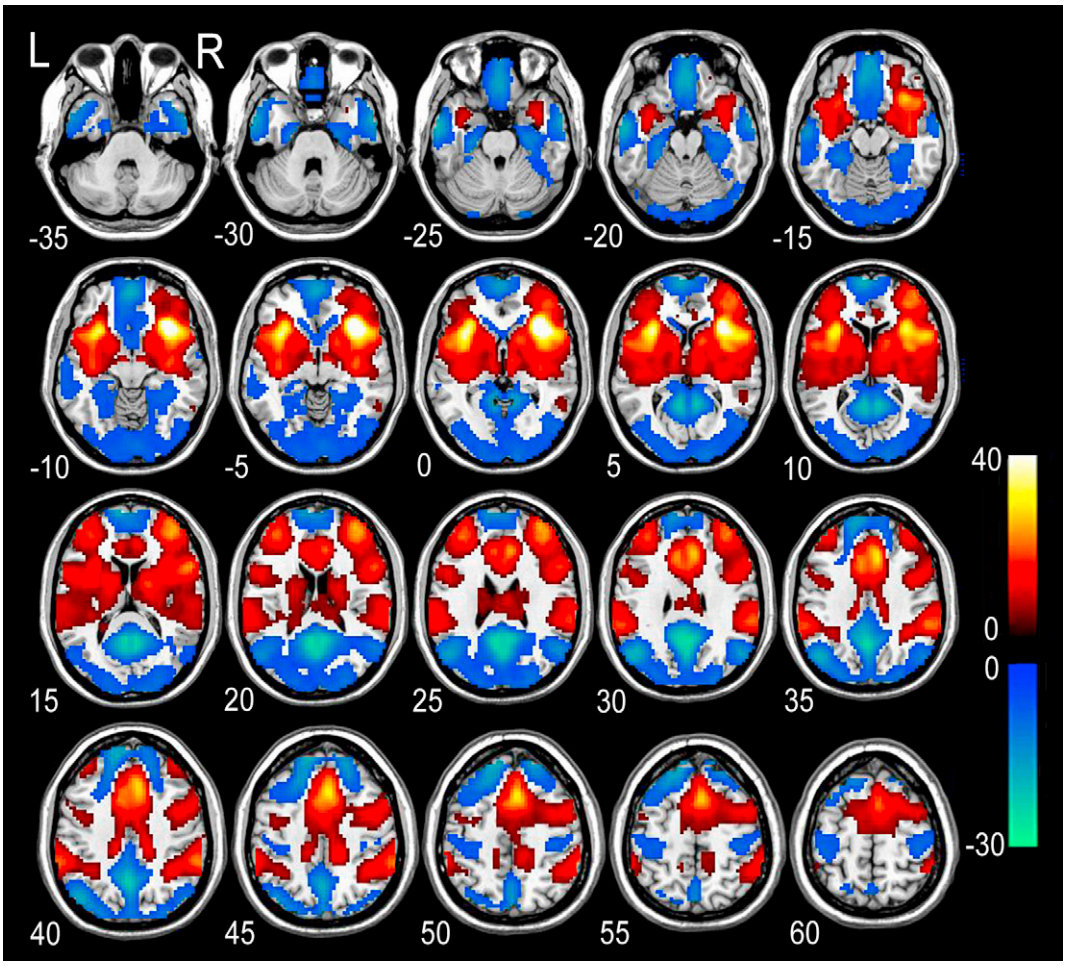

Fig. 1. The voxel-based resting-state FC map of the rFIC in 171 subjects. Red color represents positive FC; blue color denotes negative FC. Abbreviations: FC, functional connectivity; L, left; R, right; rFIC, right fronto-insular cortex.

out the effect of gender. Finally, to exclude the contribution of gray matter atrophy to the significant correlations, we re-performed ROI-based Spearman correlation analyses after further regressing out the effect of the whole brain GMV. The ROI-based correlation analyses were performed using the Statistical Package for the Social Sciences version 16.0 (SPSS, Chicago, IL, USA). A total of 13 ROIs were analyzed, and multiple comparisons were corrected using the Bonferroni method ($P < 0.05/13 = 0.0038$).

3. Results

3.1. FC patterns of the rFIC

The one-sample t test was used to reveal brain areas that had positive or negative FCs with the rFIC ($P < 0.05$, FWE corrected). Brain regions that showed positive FC with the rFIC were mainly located in the SN, CEN, and sensorimotor areas [10,25], whereas regions that showed negative FC with the rFIC were mainly located in the DMN and visual network [10,11]. The results are displayed in Fig. 1. We then defined the positive and negative FC maps as masks for the subsequent correlation analyses.

3.2. Correlations between age and positive FCs of the rFIC

We performed voxel-based non-parametric correlation analyses between age and FCs of the rFIC within the positive FC mask in all subjects with gender as a nuisance covariate. A FWE method with a threshold of $P < 0.05$ was used to correct for multiple comparisons. We found that the brain regions negatively correlated with age were mainly located in the bilateral DLPFCs, supramarginal gyri (SMG), FICs, basal ganglia (BG), and dACC (Fig. 2A). Almost all of these regions were reported as the key nodes of the CEN and SN. We further extracted six brain regions as target ROIs for ROI-based Spearman correlation analyses with age. Consistent with our hypothesis, we found significant negative correlation between age and the FC of the right FIC with each target ROI after regressing out the effect of gender, without and with atrophy correction ($P < 0.001$) (Fig. 3, Fig. S1). No areas with significant positive correlations were found in the positive FC mask using the same statistical threshold ($P < 0.05$, FWE corrected).

3.3. Correlations between age and negative FCs of the rFIC

Similarly, we performed voxel-based non-parametric correlation analyses between age and FCs of the rFIC within the negative mask in all subjects with gender as nuisance covariates ($P < 0.05$, FWE corrected). We found that the brain regions positively correlated with age were mainly located in the MPFC, PCC, left angular gyri (AG), middle temporal gyri (MTG) and parahippocampal gyri (PHG) (Fig. 2B). Almost of these regions were reported as key nodes of the DMN. We further extracted seven regions as target ROIs for ROI-based Spearman correlation analyses. Consistent with our hypothesis, we found significant positive correlation between age and the FC of the rFIC with each target ROI after regressing out effect of gender without and with atrophy correction ($P < 0.001$) (Fig. 3, Fig. S1). No areas with significant negative correlations were

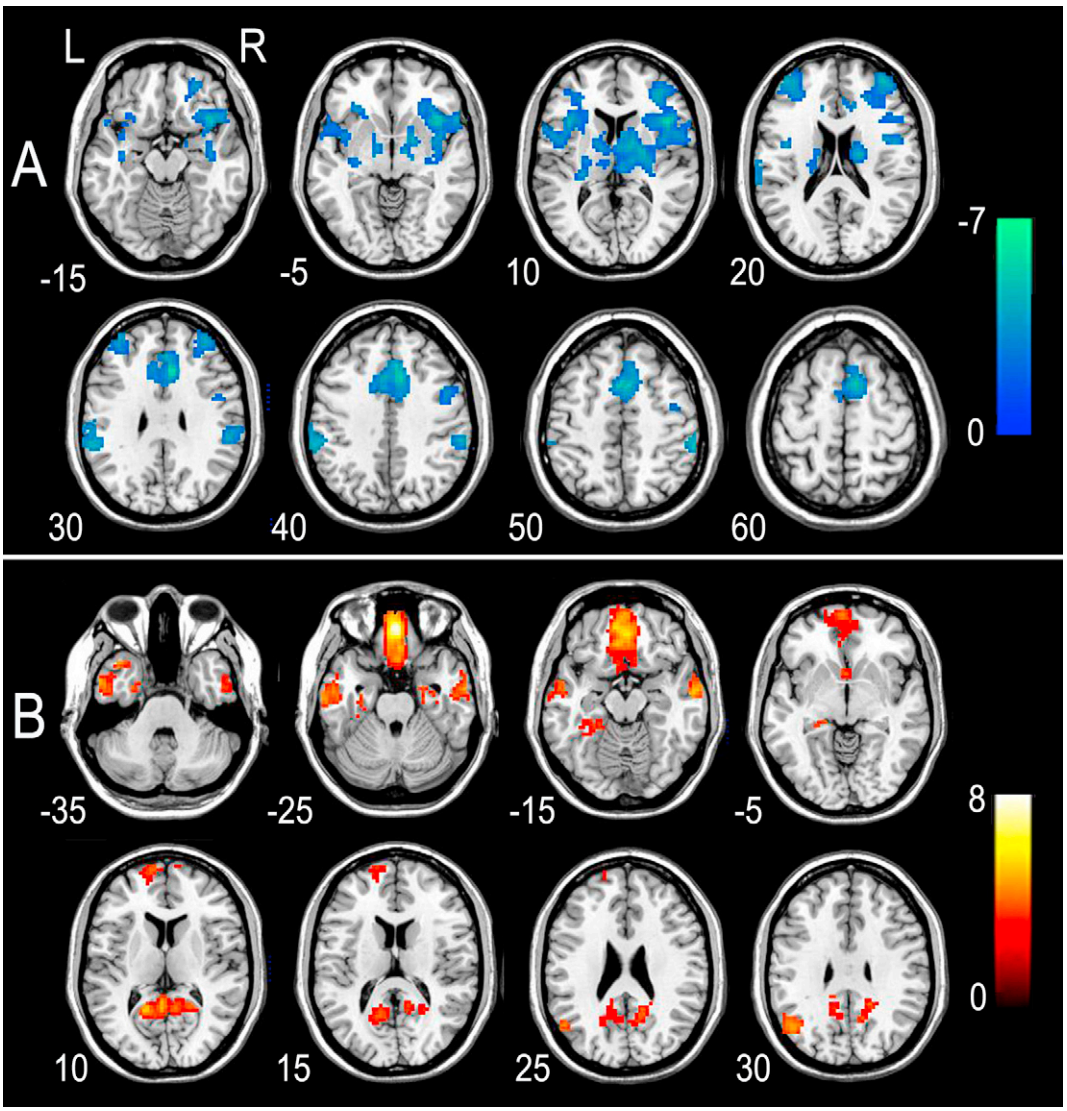

Fig. 2. Non-parametric correlation analyses controlling for gender show brain regions whose FCs with the rFIC are significantly correlated with age. (A) Search within the positive FC mask of the rFIC; (B) search within the negative FC mask of the rFIC. Red color represents positive correlation; blue color denotes negative correlation. Abbreviations: FC, functional connectivity; L, left; R, right; rFIC, right fronto-insular cortex.

found in the negative FC mask using the same statistical threshold ($P < 0.05$, FWE corrected).

4. Discussion

In the present study, using a voxel-based resting-state FC analysis, we found that the FC strengths between the rFIC and brain regions within the CEN and DMN were gradually decreased in adults from youth to middle age even after atrophy correction. These findings suggest the disconnection of the rFIC with the CEN and DMN in middle-aged subjects, which may influence the function of the rFIC in switching between the two networks.

4.1. Age-related decreases in FCs of the rFIC with the SN regions

The rFIC showed positive FCs with brain regions belonging to the CEN, SN, auditory and sensorimotor networks; however, only brain regions of the SN and CEN showed decreased FCs with the rFIC with increase of age. The SN serves to identify the most relevant among several internal and external stimuli to guide behavior [19,25]. Specifically, the FICs serve to identify salient stimuli from various sensory inputs and the rFIC also enables cognitive processing by initiating appropriate control signals. The functional disconnection of the rFIC with other nodes (such as the dACC and basal ganglions) of the SN in middle-aged subjects may help to explain previous findings of declines in perception capacity [6], attraction to novelty [16], and responsiveness to novelty and altered processing of rare targets in older subjects [28]. The dACC has been reported to be involved in a variety of cognitive functions, such as attention control [17] and conflict monitoring [5,13]. Most of these functions have been reported to be impaired in normal aging [4,8,23], which may partly account for the functional disconnection between the rFIC and dACC. Moreover, the decreased intra-network FCs of the SN is consistent with the finding that reduced intra-network FC within the SN is an important feature for distinguishing subjects with different ages in previous studies [18,21]. Taken together, these findings suggest that the decreased SN connectivity itself might be a source of age-related functional declines in attention, motor control and inhibition modulation in cognitive processing.

4.2. Relationships among the SN, CEN, and DMN

During goal-directed cognitive tasks, brain regions of the CEN (DLPFC and PPC) and SN (FIC and dACC) were activated, whereas

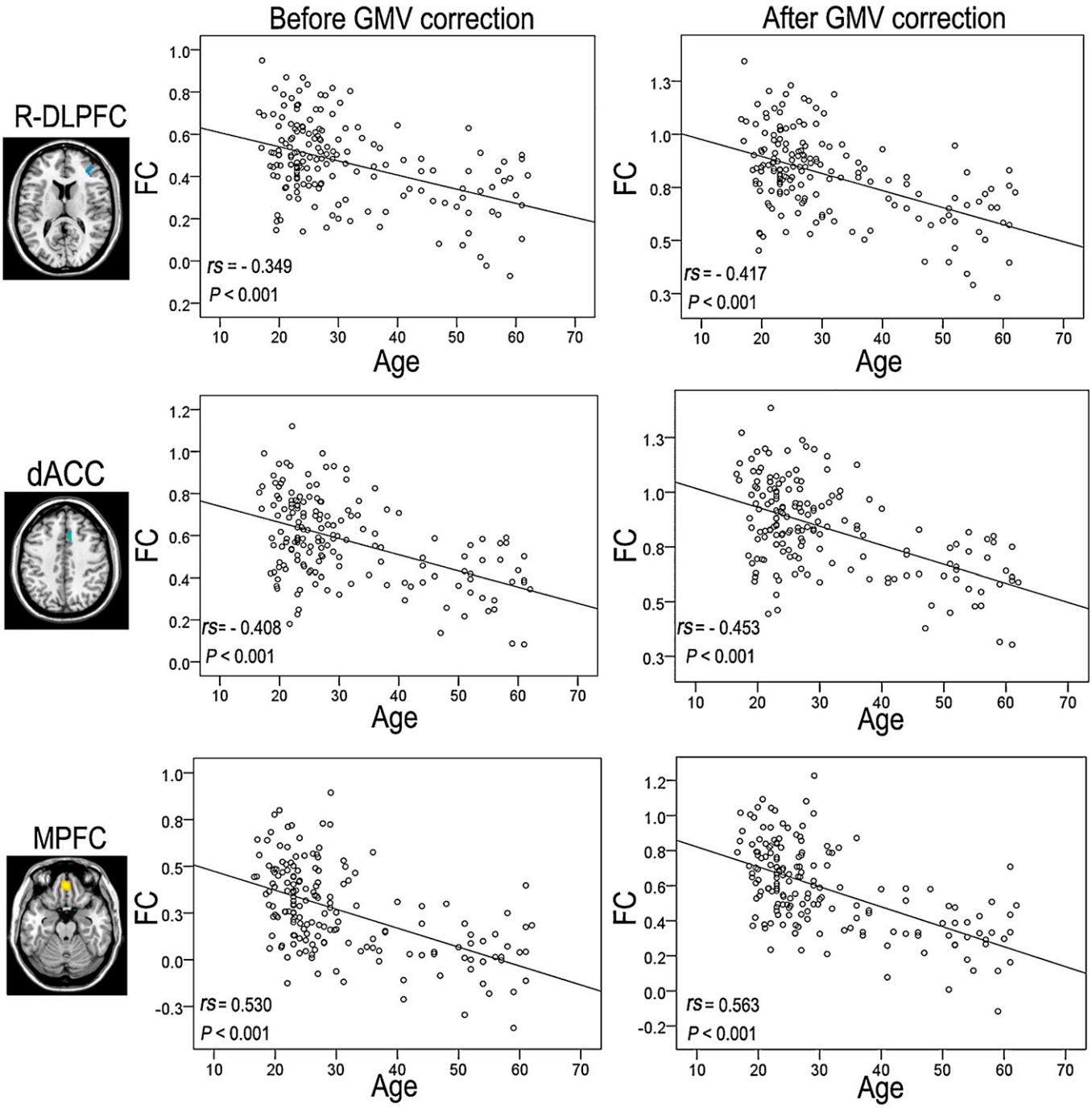

Fig. 3. Scatter plots show significant correlations between age and FCs of the rFIC with key nodes of the CEN (A), the SN (B), and the DMN (C) after regressing out the effect of gender without and with atrophy correction. Abbreviations: CEN, central executive network; dACC, dorsal anterior cingulate cortex; DMN, default mode network; FC, functional connectivity; GMV, gray matter volume; MPFC, medial prefrontal cortex; R-DLPFC, right dorsolateral prefrontal cortex; rFIC, right fronto-insular cortex; *rs*, Spearman correlation coefficients; SN, salience network.

brain regions of the DMN (MPFC/ACC and PCC/Pcu) were deactivated; the former regions were named the "task-positive network" and the latter regions were named the "task-negative network" [29]. During rest, the brain regions of the task-positive network were temporally correlated with each other and could be further divided into the SN and CEN. Brain regions of the task-negative network, however, showed high activity during rest and were also correlated with each other and identified as the DMN. Both during cognitively demanding tasks and during rest, activity in the SN and CEN and that in the DMN were negatively correlated with each other, a phenomenon which has been associated with the performance of cognitive functions [10,11,24]. The CEN is critical for the active maintenance and manipulation of information in working memory and for judgment and decision-making in the context of goal directed behavior [15,22]. The DMN serves to process self-related information [24]. It has recently been noted that the rFIC plays a critical role in switching between the CEN and the DMN [26]. Specifically, the rFIC serves to identify salient stimuli and initiates the appropriate transient control signals to engage the CEN in higher order cognitive processes while disengaging the DMN [1,19].

Importantly, the switching mechanism helps to focus attention on external stimuli and contributes to effective coordination of activity in the CEN and DMN.

Because the CEN and DMN are crucial for cognitive processing, several studies have investigated the alterations in FCs within the two networks during aging. Decreased intra-network FCs in both the CEN [21,27,29] and the DMN [2,7,9,14] have been reported in normal aging. These findings suggest that aged people have deficits in exchanging information within the two networks, which may be related to cognitive decline in these elder subjects.

4.3. Age-related FC decreases of the rFIC with the CEN and DMN

The most important finding of the present study is that the FCs of the rFIC with both the CEN and DMN were decreased with aging even in middle-aged adults. The rFIC has been shown to initiate appropriate control signals that enable a switch between the CEN and DMN in response to cognitive demands [26], which is critically important for cognitive function. For example, during a cognitively demanding task, the rFIC identifies the external stimulus and then initiates transient control signals to engage the CEN in mediating the cognitive processes in response to the external stimulus, simultaneously disengaging the DMN and thereby pausing internal information processing. The functional disconnection of the rFIC with the CEN and DMN in healthy older individuals may result in a functional deficit in switching between the CEN and DMN that will inevitably lead to cognitive decline, as has been shown in previous studies [4,8,21,23,27]. In accordance with the role of the rFIC in switching between the CEN and DMN, a recent lesion study in humans has shown that the rFIC also has an important role in cognitive control-related task switching [12]. In the present study, we further provided evidence that the functional disconnection of the rFIC was present at an earlier stage, namely in middle-aged subjects.

5. Conclusions

In the present study, using a voxel-based resting-state FC analysis, we found the age-related FC decreases between the rFIC and the DMN and CEN in middle-aged normal adults, which may reduce the role of the rFIC in switching between the CEN and DMN. These findings may improve our understanding of the age-related cognitive decline in normal subjects.

Conflict of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neulet.2013.03.044.

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