

RESEARCH ARTICLE

Differences between child and adult large-scale functional brain networks for reading tasks

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Abstract

Reading is an important high-level cognitive function of the human brain, requiring interaction among multiple brain regions. Revealing differences between children's large-scale functional brain networks for reading tasks and those of adults helps us to understand how the functional network changes over reading development. Here we used functional magnetic resonance imaging data of 17 adults (19–28 years old) and 16 children (11–13 years old), and graph theoretical analyses to investigate age-related changes in large-scale functional networks during rhyming and meaning judgment tasks on pairs of visually presented Chinese characters. We found that: (1) adults had stronger inter-regional connectivity and nodal degree in occipital regions, while children had stronger inter-regional connectivity in temporal regions, suggesting that adults rely more on visual orthographic processing whereas children rely more on auditory phonological processing during reading. (2) Only adults showed between-task differences in inter-regional connectivity and nodal degree, whereas children showed no task differences, suggesting the topological organization of adults' reading network is more specialized. (3) Children showed greater inter-regional connectivity and nodal degree than adults in multiple subcortical regions; the hubs in children were more distributed in subcortical regions while the hubs in adults were more distributed in cortical regions. These findings suggest that reading development is manifested by a shift from reliance on subcortical to cortical regions. Taken together, our study suggests that Chinese reading development is supported by developmental changes in brain connectivity properties, and some of these changes may be domain-general while others may be specific to the reading domain.

KEYWORDS

connectivity, functional magnetic resonance imaging (fMRI), graph theory, orthography, phonology, reading development, semantics

1 | INTRODUCTION

Reading is a critical cognitive ability typically acquired during childhood. Understanding reading development is critical for educational, social, and clinical policies. Given its importance, developmental cognitive neuroscience has investigated how different regions of the human cerebral cortex develop their specificity during reading acquisition (Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003; Turkeltaub, Eden, Jones, & Zeffiro, 2002). A traditional approach towards understanding the neural underpinnings of reading development has been to investigate the change in activation level of particular local brain regions (Cao

et al., 2009, 2010; Cao, Brennan, & Booth, 2015; Price, 2012; Szafarski et al., 2006; Turkeltaub et al., 2003). For example, a previous English study reported a developmental decrease in the activation of the dorsal part of the left superior temporal gyrus in a visually presented word rhyming judgment task (Bitan et al., 2007), indicating that there was reduced reliance on phonology in English reading development. Additionally, other studies found that English reading development was characterized by increased involvement of the left fusiform gyrus in visual word form recognition (Booth et al., 2003, 2004), indicating that there was increased reliance on orthography in English reading development. As for Chinese reading, a similar developmental trend has

been found. For example, Cao et al. (2009, 2010, 2015) reported that adults showed greater activation than children in the right middle occipital gyrus on reading tasks, suggesting that adults more effectively engage the brain region involved in visual-orthographic processing of Chinese characters, while children showed greater activation than adults in the left superior temporal gyrus in a rhyming task, suggesting children rely more on phonological representations of Chinese words (Cao et al., 2009, 2010, 2015).

Reading development involves the acquisition of links between the visual word forms and the phonological and semantic information of a certain language. Therefore, it requires the interactive collaboration of multiple brain regions involved in orthographic, phonological, and semantic processing (Price, 2012; Turkeltaub et al., 2002). Therefore, reading development is not only driven by the activation of particular local brain regions, but also by the changes in the interactions between a network of brain regions that are already partially active (Johnson, 2001; Schlaggar & Church, 2009; Schlaggar & McCandliss, 2007). One general theory of cognitive development is Interactive Specialization (IS) (Johnson, 2001, 2011), which argues that the onset of a new ability is due to changes in the interactions between certain brain regions (Johnson, 2011). Therefore, to understand how the brain's organization for reading emerges, a brain connectivity approach examining the interaction and integration of multiple brain regions must be applied (Bitan, 2005; Bitan et al., 2006, 2007; Koyama et al., 2011). For example, a study investigated resting state functional connectivity of the visual word form area (VWFA) in relation to reading skill in adults and children. It reported that in adults, better reading performance was associated with stronger positive correlations between VWFA and phonology-related regions (Broca's area and the left inferior parietal lobule), whereas children exhibited negative correlations in these connections (Koyama et al., 2011). Moreover, Bitan et al. (2006) examined the role of the left inferior frontal gyrus (IFG) in modulating temporal and parietal regions in visual rhyming and spelling judgment tasks in adult and children groups. They revealed that the task-related modulation on the connection from IFG to posterior task-selective regions (lateral temporal cortex for the rhyming task and intraparietal sulcus for the spelling task) was weaker in children compared to adults. This suggests that adult reading is characterized by greater top-down cognitive control compared to children (Bitan et al., 2006). A recent longitudinal study investigated how the functional connectivity of the left posterior middle temporal gyrus (pMTG) in a visual semantic judgment task changed over development. It revealed longitudinal increases in functional connectivity between the pMTG and the inferior parietal lobule (IPL) for weak semantic association word pairs and suggested that early development of semantic representations may be facilitated by enhanced engagement of phonological short-term memory (Lee, Booth, & Chou, 2016).

Traditional functional connectivity analysis focusing only on seed regions (e.g., VWFA and IFG in the aforementioned studies) fails to give a complete picture of brain connectivity profiles. The seed regions selected in most previous studies on reading development are mainly located in the left hemisphere (Bitan, 2005; Bitan et al., 2006; Lee et al., 2016) or in classic cortical regions for reading (Koyama et al.,

2011). However, numerous studies (Banai et al., 2009; Liu et al., 2009; Price, 2012) have found that reading also involves regions beyond the left-lateralized classic reading network, such as limbic and subcortical regions (Banai et al., 2009; Hornickel, Skoe, Nicol, Zecker, & Kraus, 2009), low-level visual perception regions (Liu et al., 2009; Price, 2012; Sun, Yang, Desroches, Liu, & Peng, 2011), and high-level executive function regions (Lee et al., 2016; Price, 2012; Whitney, Jefferies, & Kircher, 2011). Therefore, a larger-scale connectivity perspective might be a more informative method for studying reading development. Graph theory, a method used extensively of late, makes it possible to understand functional connectivity in a large-scale network. In this approach, the human brain is proposed to be structurally and functionally organized into a complex network to facilitate the effective segregation and integration of information processing (Zuo et al., 2012). This network is described as a graph with nodes (brain regions) and edges (functional or structural connections) (Bullmore & Sporns, 2009, 2012). Graph theory provides a powerful statistical framework for characterizing the development of brain systems in a comprehensive manner, considering not only relationships within a given system, but also how these relationships are situated within wider network contexts (Power, Fair, Schlaggar, & Petersen, 2010).

Several studies have investigated structural (Liu et al., 2015; Qi et al., 2016) and resting-state functional brain networks (Finn et al., 2014) of atypical reading development (i.e., dyslexia) using a graph theory approach, however, no graph theory based studies have been conducted to investigate typical reading development. Nevertheless, a number of studies have investigated general cognitive development using the graph-theoretic approach and revealed interesting developmental differences in brain topological properties, the roles of specific brain regions, as well as inter-regional connectivity (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Power et al., 2010). For example, one study investigated lifespan trajectory (7–85 years old) of the network properties of human functional networks (Cao et al., 2014), and found linear decreases in modularity and inverted-U shaped trajectories of local efficiency over development. Another study revealed that subcortical areas were more strongly connected with primary sensory, association, and paralimbic areas in children, compared to young adults. Young adults, on the other hand, showed stronger cortico-cortical connectivity between paralimbic, limbic, and association areas (Supekar, Musen, & Menon, 2009). Moreover, there is a research reported increased functional connectivity among more widespread brain regions in children than young adults, indicating that functional networks in children are less specialized (Jolles, Van Buchem, Crone, & Rombouts, 2011). It is of note that the aforementioned studies mainly focused on the general development of functional networks, and therefore it is unclear whether these developmental changes are also manifested in reading acquisition.

To date, graph theory based studies on functional brain development have mainly used task-independent resting-state functional MRI (rs-fMRI). According to the economic theory of brain network organization, the brain network exhibits a "relaxed" or less costly configuration during the resting-state, while it adopts a more efficient but more costly workspace configuration during a demanding task state (Bullmore

& Sporns, 2012). A recent study compared the co-activation network configurations of 4,393 studies with resting-state network data sets and revealed substantial differences in network configuration between the two paradigms (Di, Gohel, Kim, & Biswal, 2013). The graph theoretical analysis of specific reading tasks is a more targeted method for investigating the architecture of reading development, on account of the topological properties and connectivity profiles of the functional brain networks modulated or reconfigured by reading-specific task demands.

In the current study, we aimed to examine developmental differences in the large-scale functional networks of reading tasks using graph theoretical analysis. Reading acquisition relies on the mapping from orthography to phonology, as well as the mapping from orthography to semantics (Cao et al., 2010), so we adopted the visually presented rhyming judgment (orthography-to-phonology mapping) and visually presented meaning judgment (orthography-to-semantics mapping) tasks, which have been used in our previous study (Liu et al., 2012) to examine the developmental differences in the functional network during reading. Based on previous studies, we expected adults to rely more on the connections of cortical regions, whereas we expected children to rely more on subcortical regions across both tasks, consistent with a subcortical-to-cortical shift in cognitive function. In addition, we expected adults to demonstrate larger between-task differences in connectivity patterns than children, consistent with the interactive specialization (IS) theory of brain development. Finally, we expected adults to rely more on the connections between orthographic regions while we expected children to rely more on connections between phonological regions across both tasks, consistent with studies arguing for the early importance of dorsal regions involved in phonology and later reliance on ventral regions involved in orthography.

2 | MATERIALS AND METHOD

2.1 | Participants

Seventeen adults (male: 9; ages ranged from 19 to 28 years; mean: 21.8, standard deviation (SD): 2.3) and 16 typically developing children (male: 11; ages ranged from 11 to 13 years; mean: 12, SD: 0.4) were included. The detailed demographic characteristics of the two groups are shown in Table 1. Inclusion criteria were as follows: (1) native Chinese speakers; (2) right-handed; (3) normal hearing and normal or corrected to normal vision; (4) no neurological disease or psychiatric disorders; and (5) not taking medication affecting the central nervous system. All the child participants were measured by the Character Recognition Measure and Assessment Scale for Primary School Children (CRM) (Wang & Tao, 1993) to ensure that none of them are dyslexic. Written informed consent was obtained from all participants and also from the parents of child participants. This study was approved by the Institutional Review Board at Beijing Normal University.

2.2 | Design and fMRI paradigm

2.2.1 | Experimental procedure





The children's data analyzed in the current study were collected in our previous study (Liu et al., 2012). The adults' data were newly collected

TABLE 1 Demographics and task performance of the adult and child groups

	Adults	Children	<i>p</i> value
Age (mean(SD))	21.8(2.3)	11.7(0.4)	
Gender (M/F)	9/8	11/5	.22
Rt_ACC (mean(SD))	95.1%(2.2%)	73.2%(12.1%)	<.001
Rt_RT (mean(SD))	1,202(230)	1,755(445)	<.001
Mt_ACC (mean(SD))	94.2%(3.9%)	82.2%(9.7%)	<.001
Mt_RT (mean(SD))	1,056(210)	1,492(394)	<.001
Rp_ACC (mean(SD))	99.1%(1.7%)	97.9%(3.3%)	.24
Rp_RT (mean(SD))	780(200)	1,042(324)	.01
Mp_ACC (mean(SD))	96.6%(7.5%)	96.6%(4.9%)	.99
Mp_RT (mean(SD))	747(223)	1,073(300)	<.001

Rt_ACC and Rt_RT refer to the accuracy and reaction time (ms) in character condition of the rhyming judgment task; Mt_ACC and Mt_RT refer to the accuracy and reaction time in character condition of the meaning judgment task; Rp_ACC and Rp_RT refer to the accuracy and reaction time (ms) in perceptual condition of the rhyming judgment task; Mp_ACC and Mp_RT refer to the accuracy and reaction time in perceptual condition of the meaning judgment task.

using the same procedure as used in collecting the children's data. Detailed information of the experimental procedure can be found in our previous study (Liu et al., 2012). Briefly, a rhyming judgment and a meaning judgment task were used to tap into orthography-to-phonology mapping and orthography-to-semantics mapping, respectively. In both tasks, two Chinese characters were visually presented sequentially. The presentation of all characters was 800 ms in duration, followed by a 200 ms interval between the two characters. A red fixation cross (+) appeared on the screen after the offset of the second stimulus to indicate to participants that they should make a response. The response interval was chosen amongst 2,200, 2,600, and 3,000 ms with equal probability. The participants were asked to judge whether the two characters in a pair rhymed in the rhyming judgment task or were semantically related in the meaning judgment task. They were asked to press a yes button for rhyme (or semantically related) using their right index finger or to press a no button with the right middle finger. Half of the pairs of characters rhymed (or were semantically related) and half did not.

Additionally, there were two kinds of control trials (perceptual, null) for each task, designed to account for activation due to basic visual processing and executive motor processing in the character trials (Liu et al., 2012). In the perceptual control trials, two Tibetan symbols were visually presented sequentially and the participants were asked to judge whether the pair of symbols was identical or not. They were asked to press a yes button with the right index finger for identical pairs (for example,  and ) and to press a no button with the right middle finger for different pairs (for example,  and ). Half of the pairs were identical and half were not. The Tibetan symbols were used as the perceptual control conditions in both tasks (rhyming judgment and meaning judgment tasks). The Tibetan symbols used and the

number of Tibetan trials in the perceptual conditions were identical across the two tasks so that the perceptual conditions in the two tasks were comparable, but the specific symbols within pairs were different in the two tasks to avoid repetition effects. We used Tibetan characters because none of the children were familiar with them. For the null control trials, two black fixation-crosses were visually presented sequentially. When the second black fixation-cross turned blue, participants were required to press a yes button with the right index finger during the subsequent interval. The timing for perceptual and null trials was the same as for character trials.

We used an event-related design with four 6 min 44 s runs, including two runs for each task. In each run, there were 48, 12, and 24 pairs of character stimuli, perceptual stimuli, and null stimuli, respectively. In each run, there was a 12 s equilibration period at the beginning, and a 22 s period at the end in order to allow deconvolution of the entire hemodynamic response function (HRF) of the last trial. An instruction indicating the task type (“rhyming judgment task” or “meaning judgment task”) was presented to indicate the specific experimental task at the beginning of a run. The administration of the two tasks was counterbalanced across participants. Before fMRI scanning, participants briefly practiced the tasks so that they were familiar with the experimental procedure and task requirements. To allow for adaptation to the scanning procedure and minimization of subject motion, children were familiarized with the scanning environment in a simulated MRI scanner prior to data collection.

2.2.2 | Stimulus characteristics

Several stimulus factors were controlled in the rhyming and meaning judgment tasks. First, the characters were matched for frequency, acquisition age, and number of strokes across the rhyming and meaning tasks. Second, for the rhyming judgment task, the two characters in a pair shared an identical lexical tone, so that tone would not potentially interfere with the rhyming judgment. Third, all characters were from Chinese language textbooks for primary school. Detailed information about the stimulus characteristics can be found in our previous study (Liu et al., 2012).

2.3 | Image acquisition

All images were acquired using a 3 T Siemens scanner (MAGNETOM Trio, a TIM System) at Beijing Normal University. For the functional imaging, a susceptibility weighted single-shot echo planar imaging (EPI) method with blood oxygenation level-dependent (BOLD) signal recording was adopted. The following scan parameters were used: TR = 2,000 ms; TE = 20 ms; flip angle = 80°; slice thickness = 3 mm, gap = 0.48 mm; number of slices = 32; FOV = 220 × 206 mm; matrix = 128 × 120 × 32; pixel size = 1.72 × 1.72 × 3.48 mm. In addition, a high resolution T1 weighted 3D image (MPRAGE) was acquired with the following parameters: number of axial slices = 160; slice thickness = 1 mm; FOV = 256 × 256 mm; matrix = 256 × 256 × 160; voxel size = 1 × 1 × 1 mm; TR = 2,300 ms; TE = 3.36 ms.

2.4 | Data preprocessing

Image preprocessing was first performed using DPARSF (<http://rfmri.org/DPARSF>). Image preprocessing included: slice timing, realignment, co-registration, tissue segmentation, normalization, smoothing, high-pass filtering, detrending, and regressing out potential sources of particular signals. Specifically, slice-timing correction was performed by interpolating the voxel time series using slice interpolation, and the middle slice in time was used as a reference slice. Second, all functional images were spatially realigned and co-registered to their corresponding anatomical images. No participants had more than 3.0 mm of movement within-run in any plane. The resulting images were then spatially normalized to the Montreal Neurological Institute (MNI) space. After normalization, all images were resampled to 3 × 3 × 3 mm voxel size, and were further spatially smoothed using a Gaussian kernel with 8 mm full-width at half maximum (FWHM). After those standard preprocessing procedures, three additional processes were applied for calculating functional connectivity: (1) High-pass temporal filtering with a cutoff of 1/128 Hz; (2) removing linear trends; (3) regressing out potential sources of head motion, white matter signal, and cerebrospinal fluid (CSF) signal.

2.5 | Network construction

Graph theoretical analysis was performed in GREYNA (<http://www.nitrc.org/projects/gretna/>). For each participant, the whole brain (excluding cerebellum) was partitioned into 90 regions of interest (ROI) (Figure 1a) according to the Automated Anatomical Labeling (AAL) tool (Tzourio-Mazoyer et al., 2002). Regional time series were calculated by averaging all voxel time series within the region. To construct the network for the rhyming and meaning judgment tasks, we extracted time series corresponding to Chinese character condition (Figure 1b) as described in a previous study (Liang, Zou, He, & Yang, 2015). Specifically, the relevant time points in the Chinese character trials (rhyming and meaning judgment) were extracted and concatenated over trials, similar to a previous study (Ekman, Derrfuss, Tittgemeyer, & Fiebach, 2012). Time courses were extracted from the onset of the first stimulus in a pair to one TR after the second stimulus in a pair, for each ROI and each subject. We only extracted the time series specific to the character condition. As for the control trials (null and perceptual conditions), they were used in analyses to determine task-specific maps of regional activity, which has been reported in our previous publication (Liu et al., 2012). In the current study, the behavioral data of perceptual condition were used as covariates to control for the potential impact of basic visual processing. We verified that there was no significant differences in the time series between the 2 runs for each task using paired *t* tests in each brain region of each participant, and we then concatenated the time series over runs. Pearson's correlation coefficient between each pair of regional time series was calculated, resulting in a 90 × 90 connectivity matrix for each participant per task (Figure 1c). Due to the ambiguous biological explanation of negative correlations (Fox et al, 2009; Murphy et al, 2009), we restricted our analysis to positive correlations. Binary matrices *B* (Figure 1d) were generated from the connectivity matrix of each participant using different values of a sparsity

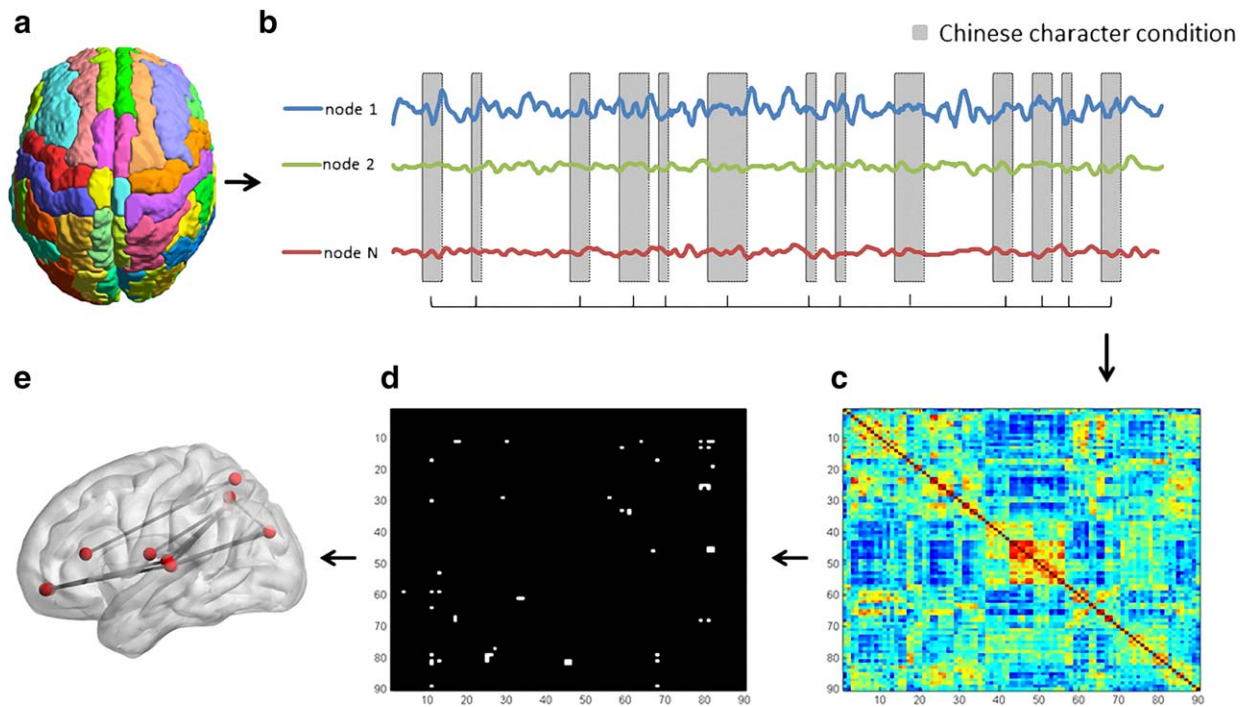


FIGURE 1 Schematic of functional network construction. (a) Use Automated Anatomical Labeling (AAL) template to divide the whole brain into 90 nodes by averaging all voxel time series within each node; (b) Time series from the Chinese character condition for each task were extracted for each node; (c) Time series concatenated over runs to calculate pairwise correlation matrices for each subject and task; (d) Binary matrix was generated from the correlation matrix for each subject and task; (e) Visualization of the functional network in the character condition for each task after regressing out confounding factors and FDR correction [Color figure can be viewed at wileyonlinelibrary.com]

threshold. b_{ij} was set to 1 if the absolute value of the correlation coefficient between regions i and j ($i \neq j$) was above the sparsity threshold; otherwise, it was set to 0. We applied a set of sparsity thresholds (ranging from 0.05 to 0.4, with a step size of 0.01) to binarize networks. This range of sparsity threshold was chosen because networks were not fully connected at lower sparsity values and were less likely to maintain small-world architecture at higher sparsity values, as demonstrated in previous studies (Achard, 2006; Liang et al., 2015). Lastly, we visualized the task-specific networks after regressing out confounding factors and FDR correction (Figure 1e).

2.6 | Graph theoretical analysis

Graph theoretical measures were used to characterize the topological architectures of the functional brain networks derived above. In the current study, network properties including both global and nodal properties, which have been frequently used in previous studies on brain network analysis (Cao et al., 2014; Liu et al., 2016; Qi et al., 2016), were analyzed for each task's network. The global measures were included to reveal the architecture of the entire network, whereas nodal measures were included to interpret the contributions of individual nodes or brain regions to the network.

2.6.1 | Global properties

Global efficiency

This parameter measures the parallel information transfer ability in the network. A network with high global efficiency possesses superior

ability to combine specialized information from distributed brain regions (Rubinov & Sporns, 2010). Specifically, for a network G with N nodes, the average shortest path length between all pairs of nodes in the network is known as the characteristic path length of the network (Watts & Strogatz, 1998). The average inverse of the characteristic path length between each pair of nodes within the network is defined as the global network efficiency (Latora & Marchiori, 2001).

$$E_{\text{global}}(G) = \frac{1}{N(N-1)} \sum_{i \neq j \in G} \frac{1}{d_{ij}}$$

where N is the number of total nodes in network G , and d_{ij} is the characteristic path length between nodes i and j in the network (Latora & Marchiori, 2001, 2003).

Local efficiency

This parameter measures the information exchange ability among a subgraph with locally connected nodes. A network with high local efficiency is characterized by the presence of closely interconnected clusters, suggesting the potential for functional segregation in these clusters (Latora & Marchiori, 2001; Rubinov & Sporns, 2010). For a network G with N nodes, the local efficiency is defined as the average (across nodes) of the global efficiencies of the subgraphs consisting of each node and its neighbors (Latora & Marchiori, 2001).

$$E_{\text{loc}}(G) = \frac{1}{N} \sum_{i \in G} E_{\text{global}}(G_i)$$

where G_i is the subgraph consisting of node i and its neighbors and $E_{\text{global}}(G_i)$ is the global efficiency of G_i (Latora & Marchiori, 2001).

2.6.2 | Nodal properties

Nodal Degree

Degree (k_i) of a particular node is the number of other nodes that directly connect to that node, i.e., the number of edges that connect it to the rest of the network. Highly connected nodes have large degree. Normalized k_i is obtained by dividing a given node's k_i by the mean k_i of the whole network. Degree reveals the importance of a given node in the network.

Hubs

Hubs of a functional network are crucial nodes that can be defined by various methods (Sporns & Honey, 2007). In the current study, we chose degree to define the hubs of the network, as in our previous study (Qi et al., 2016). If the normalized degree of a node was 1.5 SD greater than the mean degree across all nodes in the network, the node was defined as a hub in the network.

2.7 | Statistical analysis

2.7.1 | Group and task differences in inter-regional correlations

We used a surrogate data analysis to estimate the statistical significance of pair-wise functional correlations (Corp, 1997) for the rhyming and meaning judgment tasks. First, 1000 surrogate bold time series were generated for each region (e.g., AAL 01) by randomizing the phase of the original time series. Second, we calculated the significance in a manner similar to the bootstrap method. We correlated these random-phase series (1000) of each region (e.g., AAL 01) with the time series of other regions (e.g., AAL 02). These 1000 correlation coefficients formed a distribution, and if the observed pair-wise correlation coefficients were larger than the 95th percentile of the corresponding surrogate distribution, it was considered to be statistically significant. This method circumvents the need to match groups on network sparsity, and is also better for dealing with time series that are serially correlated (Corp, 1997).

To reveal whether there were significant between-group differences in the pair-wise functional connectivity for the rhyming and meaning judgment tasks, we first identified the statistically significant pairs either in the adult group or the child group (a union of statistically significant maps of both age groups), and then used two sample *t*-tests to assess the between-group differences of inter-regional correlations. We regressed out covariates of sex and reaction time of the perceptual control condition in between-group analysis by using an ANCOVA to control the potential impact of sex difference and basic visual recognition ability. Reaction time rather than accuracy of perceptual control condition was controlled as the between-group difference was only significant in reaction time but not in accuracy as shown in Table 1. After that, FDR correction was performed at an alpha level of 0.05 to correct for multiple comparisons. The same method was used to examine between-task differences in the pair-wise functional connectivity for both groups. We used paired sample *t*-tests, but did not regress out reaction time or response accuracy of perceptual control condition, as there were no significant between-task differences in reaction time or

accuracy in the adult (reaction time: $t(16) = 1.368, p = .190$; accuracy: $t(16) = 1.269, p = .223$) or the child group (reaction time: $t(15) = -0.980, p = .343$; accuracy: $t(15) = 1.344, p = .199$).

2.7.2 | Group differences in network global properties

To examine whether there were significant group differences in global network efficiency and local network efficiency, we used ANCOVA with sex and reaction time in the perceptual control condition as two covariates to compare the values of these properties. We repeated this analysis over a range of sparsity thresholds (from 0.05 to 0.4) and computed the area under the curve (AUC, curves are global network efficiency vs sparsity threshold and local network efficiency vs sparsity threshold) for the rhyming and meaning judgment tasks separately. We also conducted permutation tests (FDR-corrected) to validate the findings of this analysis (Nichols & Holmes, 2001).

2.7.3 | Group and task differences in nodal properties

We calculated the AUC for nodal degree (curve is degree vs sparsity threshold) to obtain measures for nodal topology that were independent of a single threshold (Bassett, Nelson, Mueller, Camchong, & Lim, 2012). Following this, we tested whether there were significant group or task differences in each node's degree using two sample or paired sample *t*-tests, respectively. In addition, we regressed out the covariates of sex and the reaction time in perceptual control condition by using an ANCOVA to control for potential sex and visual processing differences in between-group analysis. Finally, an FDR correction was conducted at an alpha level of 0.05 to correct for multiple comparisons.

3 | RESULTS

3.1 | Developmental differences in global network properties

We did not find any between-group differences in global network properties (global efficiency and local efficiency) for either the rhyming or meaning judgment task over the range of thresholds (from 0.05 to 0.4).

3.2 | Developmental and task differences in inter-regional correlations

The significant inter-regional connectivity map for both groups and tasks as well as the common inter-regional connectivity map across both groups are shown in Supporting Information Figure S1. As can be seen from this figure, adults and children had extensive significant inter-regional connections common across tasks.

The between-group differences in inter-regional correlations in the rhyming judgment task are shown in Table 2 and Figure 2 (upper row). Thirty two pairs of regions showed significant between-group differences ($p < .05$, FDR-corrected) in the rhyming judgment network, after controlling for the effects of sex and reaction time of perceptual condition. Specifically, adults had greater inter-regional correlations than children mainly in the left hemisphere, including correlations between

TABLE 2 Pairs of regions showing significant group differences in inter-regional correlations in the rhyming judgment task

	Region A	Region B	A	C	<i>p</i> value
A>C	Inferior occipital gyrus.L	Fusiform gyrus.L	0.56	0.42	.012
	Inferior occipital gyrus.L	Fusiform gyrus.R	0.45	0.20	.007
	Inferior occipital gyrus.L	Precentral gyrus.L	0.39	0.16	.001
	Middle occipital gyrus.R	Fusiform gyrus.R	0.51	0.28	.001
	Inferior parietal lobule.L	Inferior frontal gyrus(oper).L	0.48	0.26	.006
	Inferior parietal lobule.L	Inferior frontal gyrus(tri).L	0.47	0.19	.004
	Superior parietal gyrus.L	Precentral gyrus.L	0.42	0.16	.008
	Middle frontal gyrus.L	Middle frontal gyrus(orb).L	0.54	0.42	.035
	Superior frontal gyrus(dor).R	Superior frontal gyrus(med).R	0.67	0.53	.01
	Precentral gyrus.R	Paracentral lobule.L	0.47	0.29	.001
	Superior frontal gyrus(med).L	Anterior cingulate and paracingulate gyri.L	0.60	0.47	.035
	Superior frontal gyrus(med).R	Anterior cingulate and paracingulate gyri.L	0.57	0.39	.003
	Superior frontal gyrus(med).L	Anterior cingulate and paracingulate gyri.R	0.55	0.39	.01
	Superior frontal gyrus(med).R	Anterior cingulate and paracingulate gyri.R	0.63	0.44	.001
	Superior frontal gyrus(dor).R	Anterior cingulate and paracingulate gyri.R	0.50	0.31	.001
	Superior frontal gyrus(med orb).L	Anterior cingulate and paracingulate gyri.R	0.45	0.27	.013
	Superior frontal gyrus(med orb).R	Anterior cingulate and paracingulate gyri.R	0.59	0.35	.004
C>A	Superior temporal gyrus.L	Insula.L	0.39	0.56	.006
	Superior temporal gyrus.L	Insula.R	0.44	0.55	.049
	Heschl gyrus.R	Rolandic operculum.L	0.37	0.52	.013
	Heschl gyrus.R	Rolandic operculum.R	0.53	0.67	.006
	Insula.L	Inferior frontal gyrus(oper).L	0.22	0.47	.002
	Insula.L	Inferior frontal gyrus(tri).L	0.18	0.38	.008
	Insula.L	Rolandic operculum.L	0.46	0.61	.004
	Insula.R	Supramarginal gyrus.L	0.23	0.38	.023
	Insula.R	Lenticular nucleus, pallidum.R	0.16	0.37	.01
	Lenticular nucleus, putamen.R	Rolandic operculum.R	0.21	0.35	.019
	Lenticular nucleus, putamen.R	Lenticular nucleus, pallidum.R	0.51	0.62	.116
	ParaHippocampal gyrus.L	ParaHippocampal gyrus.R	0.52	0.63	.036
	Hippocampus.L	ParaHippocampal gyrus.R	0.42	0.53	.027
	Superior parietal gyrus.L	Superior parietal gyrus.R	0.46	0.65	.007
	Posterior cingulate gyrus.L	Precuneus.L	0.42	0.60	.023

Pairs of regions with significant group differences in the rhyming judgment task obtained by two sample *t* tests (FDR-corrected, $p < .05$). tri = triangular part, oper = opercular part, orb = orbital part, med = medial, dor = dorsolateral, med orb = medial orbital. A, adults; C, children; L, left; R, right.

occipital and temporal regions (e.g., between inferior/middle occipital gyrus (IOG/MOG) and fusiform gyrus (FFG)), between occipito-parietal visual spatial regions and frontal regions (e.g., between inferior parietal lobule (IPL) and inferior frontal gyrus (IFG), between superior parietal gyrus (SPG) and precentral gyrus (PreCG)). Adults also had greater inter-regional connectivity than children between bilateral anterior cingulate and paracingulate gyri (ACG) and bilateral superior frontal gyri (SFG). In contrast, children had stronger inter-regional correlations than adults more bilaterally, mainly between left superior temporal gyrus (STG) and bilateral insula (INS), between left INS and left IFG, between right Heschl's gyrus (HES) and bilateral rolandic operculum (ROL) as well as between left INS and left ROL. Children also had greater inter-regional connectivity than adults in subcortical and limbic regions, including connections between right INS and right pallidum (PAL), right putamen (PUT) and right PAL, between right PUT and right ROL, as well as between left parahippocampal gyrus (PHG)/hippocampus (HIP) and right PHG.

The group differences in inter-regional correlations in the meaning judgment task are shown in Table 3 and Figure 2 (lower row). Similar to the rhyming task, adults had greater inter-regional correlations than children between occipital-temporal visual orthographic regions (e.g.,

between bilateral IOG; between right MOG and right FFG), as well as between temporo-parietal regions and frontal regions (e.g., between right IPL and right middle frontal gyrus (MFG), between left inferior temporal gyrus (ITG) and left IFG). Adults also had greater inter-regional connectivity than children between bilateral middle cingulate and paracingulate gyri (DCG) and right posterior cingulate gyrus (PCG), between right DCG and right precuneus (PCUN). In contrast, children mainly had greater inter-regional correlations than adults between subcortical and cortical regions, as well as between subcortical regions, including connections between bilateral INS and left ROL, between bilateral INS and basal ganglia regions (bilateral PUT and PAL), between right PUT and right PAL, as well as between left PUT and left thalamus (THA). In addition, children had greater inter-regional correlations among frontal regions (e.g., between left SFG and its right homologous region, between right SFG and left MFG).

Between-task differences in inter-regional correlations were only found in the adult group, which is shown in Table 4 and Figure 3. Thirty three pairs of regions showed significant task differences ($p < .05$, FDR-corrected). Specifically, the rhyming judgment task had greater inter-regional correlations than the meaning judgment task mainly located in left hemisphere, including connections between left parieto-

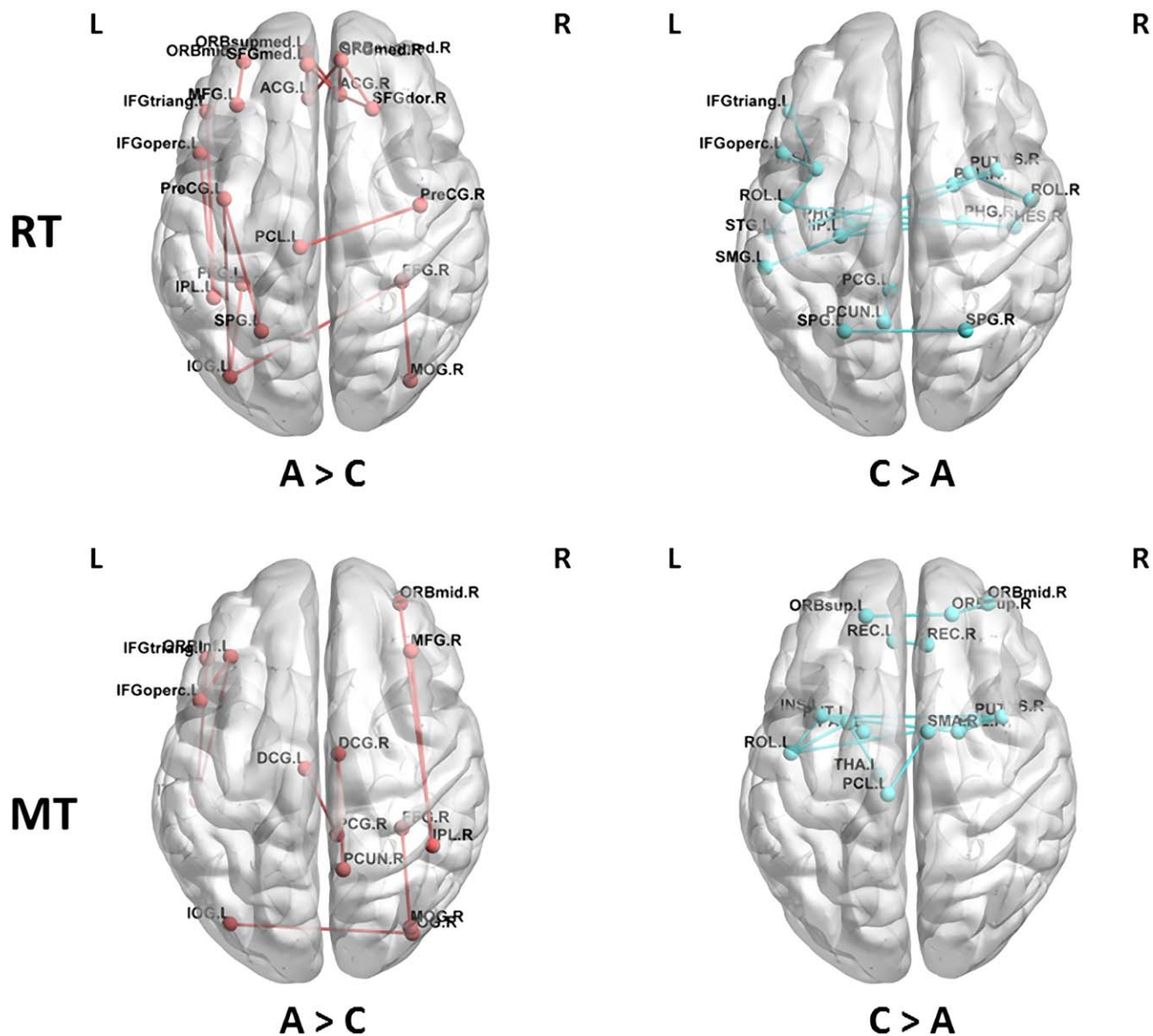


FIGURE 2 Between-group differences in inter-regional correlation in the rhyming judgment task (upper row) and the meaning judgment task (lower row). The alpha level for significant between-group differences was set at $p < .05$ (FDR-corrected). RT, rhyming judgment task; MT, meaning judgment task; A, adults; C, children; L, left; R, right. See Appendix table for abbreviations [Color figure can be viewed at wileyonlinelibrary.com]

occipital regions (left IPL, SPG and IOG) and left frontal cortex (left IFG and PreCG), between temporal regions (bilateral middle temporal gyri (MTG) & bilateral temporal pole (TPOmid)) and bilateral SFG. The rhyming task also had stronger connectivity than the meaning judgment task between bilateral SFG, as well as between bilateral SFG and cingulate regions (bilateral ACG and left PCG). In contrast, the meaning judgment task had greater inter-regional correlations mainly between the orbital part of left IFG and the triangular/opercular part of left IFG and between several brain regions in the right hemisphere (e.g., between the orbital part of right MFG and the orbital part of right SFG, between right STG and right HES, as well as between right STG/HES and right ROL).

Of note, we did not find any task differences in inter-regional correlations for the child group, even when the p value of FDR correction was set to 0.1.

3.3 | Developmental and task differences in network nodal degree

Group differences in regional network properties (nodal degree) were investigated for the rhyming judgment and meaning judgment networks by computing the AUC of nodal degree (curve is sparsity threshold vs nodal degree) as described in the methods section.

The between-group differences in nodal degree in the rhyming and meaning judgment tasks are shown in Table 5 and Figure 4. For the rhyming judgment network, adults had significantly higher degree than children in bilateral visual occipital regions (bilateral cuneus (CUN), left IOG, left calcarine fissure (CAL) and surrounding cortex), left SPG, right SFG, and right postcentral gyrus (PoCG), yet they showed significantly lower degree in several subcortical brain regions (bilateral INS, PUT, PAL and THA), as well as some other regions (left ROL, left PCUN

TABLE 3 Pairs of regions showing significant group differences in inter-regional correlations in the meaning judgment task

	Region A	Region B	A	C	p value	
A>C	Inferior occipital gyrus.L	Inferior occipital gyrus.R	0.73	0.57	.014	
	Middle occipital gyrus.R	Fusiform gyrus.R	0.48	0.24	.010	
	Inferior parietal lobule.R	Middle frontal gyrus.R	0.69	0.55	.003	
	Inferior parietal lobule.R	Middle frontal gyrus(orb).R	0.50	0.30	.014	
	Inferior temporal gyrus.L	Inferior frontal gyrus(tri).L	0.45	0.12	.003	
	Inferior temporal gyrus.L	Inferior frontal gyrus(orb).L	0.40	0.14	.007	
	Inferior frontal gyrus(oper).L	Inferior frontal gyrus(tri).L	0.83	0.76	.045	
	Inferior frontal gyrus(oper).L	Inferior frontal gyrus(orb).L	0.53	0.36	.050	
	Middle cingulate and paracingulate gyri.L	Posterior cingulate gyrus.R	0.50	0.24	.001	
	Middle cingulate and paracingulate gyri.R	Posterior cingulate gyrus.R	0.47	0.20	<.001	
	Middle cingulate and paracingulate gyri.R	Precuneus.R	0.46	0.19	.004	
	C>A	Insula.L	Rolandic operculum.L	0.46	0.65	.001
		Insula.R	Rolandic operculum.L	0.34	0.55	.005
Insula.L		Insula.R	0.58	0.70	.047	
Insula.L		Lenticular nucleus, putamen.L	0.28	0.59	<.001	
Insula.R		Lenticular nucleus, putamen.R	0.23	0.56	<.001	
Insula.L		Lenticular nucleus, pallidum.L	0.20	0.45	.002	
Insula.L		Lenticular nucleus, pallidum.R	0.12	0.41	<.001	
Insula.R		Lenticular nucleus, pallidum.R	0.11	0.42	<.001	
Lenticular nucleus, putamen.R		Lenticular nucleus, pallidum.R	0.49	0.62	.011	
Lenticular nucleus, putamen.L		Thalamus.L	0.30	0.45	.003	
Lenticular nucleus, putamen.L		Rolandic operculum.L	0.20	0.41	.010	
Superior frontal gyrus(orb).L		Superior frontal gyrus(orb).R	0.45	0.63	.023	
Superior frontal gyrus(orb).R		Middle frontal gyrus(orb).L	0.30	0.50	.011	
Gyrus rectus.L		Gyrus rectus.R	0.66	0.76	.004	
Paracentral lobule.L		Supplementary motor area.R	0.38	0.52	.021	

Pairs of regions with significant group differences in the meaning judgment task obtained by two sample *t* tests (FDR-corrected, $p < .05$). tri = triangular, orb = orbital, oper = opercular part. A, adults; C, children; L, left; R, right.

and left supramarginal gyrus (SMG)) (Table 5 and upper 2 rows of Figure 4). For the meaning judgment network, adults had significantly higher degree in left MTG and right CUN, HIP and PreCG, yet they showed significantly lower degree in several subcortical brain regions (bilateral PUT, PAL, THA and left INS) (Table 5 and lower 2 rows of Figure 4).

Similar to the pattern of task differences in inter-regional correlation, only the adult group showed significant task differences in nodal degree (Figure 5) after FDR correction ($p < .05$). Specifically, the rhyming judgment task had higher nodal degree in right SFG (rhyming task = 9.192, meaning task = 8.253, $p = .017$) and left IOG (rhyming task = 6.725, meaning task = 5.550, $p = .014$) than in the meaning task, while the meaning judgment task had higher degree in right PHG than in the rhyming task (rhyming task = 6.602, meaning task = 7.826, $p = .022$).

3.4 | Developmental differences in the distribution of hubs

In the rhyming judgment task, there were 9 regions identified as hubs (nodes with normalized degree 1.5 SD higher than mean degree across all nodes) in the adult group (Table 6 and upper two rows of Figure 6). Within these regions, prefrontal regions consisted of the greatest proportion of the hubs (56% of the total). In the child group, however, 6 regions were identified as hubs, 67% of which were situated in subcortical regions. Only one region – the left anterior cingulate and

paracingulate gyri – was defined as a common hub across both the adult and child groups.

In the meaning judgment task, over half of the hubs were in temporal regions (60%), and the remaining were in prefrontal regions in the adult group. However, in the child group, 71% of hubs were located in subcortical regions (Table 6 and lower two rows of Figure 6). No regions were identified as common hubs across groups in this task.

4 | DISCUSSION

In this study, we explored the developmental differences in the organization of the whole-brain functional network supporting Chinese reading-related tasks. Our study is the first to examine typical reading development from the perspective of large-scale brain connectivity in more than one task. Specifically, we used graph theoretical analysis to evaluate the topological properties and inter-regional connectivity of functional networks activated in rhyming judgment and meaning judgment tasks in adults and children. Our major findings were as follows: (1) Reading development is characterized by increased reliance on regions of visual orthographic processing, and decreased reliance on regions of auditory phonological processing across both tasks. (2) The functional brain networks in reading-related tasks become more specialized over development. Specifically, only adults showed between-task differences in inter-regional connectivity and nodal degree, while children did not show these differences. (3) Reading development is

TABLE 4 Pairs of regions showing significant task differences in inter-regional correlations in the adult group

	Region A	Region B	RT	MT	p value	
RT>MT	Inferior parietal lobule.L	Inferior frontal gyrus(oper).L	0.48	0.38	.035	
	Inferior parietal lobule.L	Inferior frontal gyrus(tri).L	0.47	0.31	.018	
	Inferior parietal lobule.L	Superior parietal gyrus.L	0.64	0.53	.022	
	Superior parietal gyrus.L	Precentral gyrus.L	0.42	0.32	.024	
	Inferior occipital gyrus.L	Precentral gyrus.L	0.39	0.30	.030	
	Angular gyrus.L	Angular gyrus.R	0.64	0.52	.030	
	Middle temporal gyrus.L	Superior frontal gyrus(oper).L	0.42	0.21	.014	
	Middle temporal gyrus.R	Superior frontal gyrus(oper).R	0.45	0.30	.035	
	Temporal pole: middle temporal gyrus.L	Superior frontal gyrus(oper).L	0.46	0.30	.014	
	Temporal pole: middle temporal gyrus.R	Superior frontal gyrus(oper).R	0.31	0.20	.034	
	Inferior frontal gyrus(oper).L	Precentral gyrus.L	0.62	0.53	.029	
	Superior frontal gyrus(oper).L	Superior frontal gyrus(oper).L	0.65	0.55	.001	
	Superior frontal gyrus(oper).R	Superior frontal gyrus(oper).R	0.52	0.36	.002	
	Superior frontal gyrus(oper).L	Superior frontal gyrus(oper).L	0.59	0.50	.024	
	Superior frontal gyrus(oper).R	Superior frontal gyrus(oper).R	0.81	0.77	.048	
	Superior frontal gyrus(oper).L	Superior frontal gyrus(oper).L	0.52	0.40	.022	
	Superior frontal gyrus(oper).R	Superior frontal gyrus(oper).R	0.80	0.70	.002	
	Superior frontal gyrus(oper).L	Anterior cingulate and paracingulate gyri.L	0.60	0.48	.007	
	Superior frontal gyrus(oper).R	Anterior cingulate and paracingulate gyri.L	0.57	0.47	.029	
	Superior frontal gyrus(oper).L	Anterior cingulate and paracingulate gyri.R	0.55	0.43	.021	
	Superior frontal gyrus(oper).R	Posterior cingulate gyrus.L	0.39	0.28	.028	
	Superior frontal gyrus(oper).L	Gyrus rectus.L	0.53	0.43	.015	
	Superior frontal gyrus(oper).R	Olfactory cortex.R	0.47	0.35	.045	
	Superior frontal gyrus(oper).L	Gyrus rectus.R	0.73	0.66	.030	
	MT>RT	Inferior frontal gyrus(orb).L	Inferior frontal gyrus(oper).L	0.32	0.53	.004
		Inferior frontal gyrus(orb).L	Inferior frontal gyrus(tri).L	0.46	0.68	.001
		Middle frontal gyrus.R	Superior frontal gyrus(dor).R	0.44	0.55	.029
		Middle frontal gyrus(orb).R	Superior frontal gyrus(orb).R	0.53	0.63	.029
		Superior temporal gyrus.R	Rolandic operculum.R	0.52	0.62	.023
		Superior temporal gyrus.R	Heschl gyrus.R	0.52	0.60	.032
Heschl gyrus.L		Rolandic operculum.R	0.41	0.47	.029	
Rolandic operculum.R		Postcentral gyrus.R	0.47	0.56	.025	
Precentral gyrus.R		Postcentral gyrus.R	0.66	0.73	.031	

Pairs of regions with significant task differences in the adult group obtained by paired sample t tests (FDR-corrected, $p < .05$). dor = dorsolateral, oper = opercular, tri = triangular, med = medial, med orb = medial orbital, orb = orbital. MT, meaning judgment task; RT, rhyming judgment task; L, left; R, right.

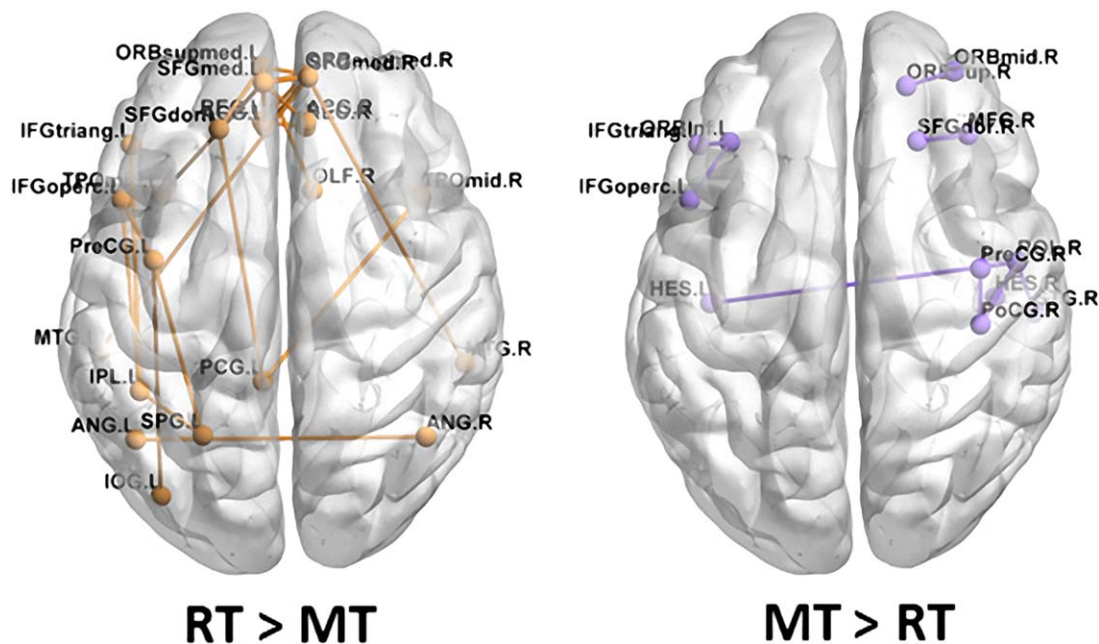


FIGURE 3 Between-task differences in the inter-regional correlations in the adult group. The alpha level for significant task differences was set at $p < .05$ (FDR-corrected). RT, rhyming judgment task; MT, meaning judgment task; L, left; R, right. See Appendix table for abbreviations [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 5 Group differences of nodal degree in two tasks

		Region	A_Degree	C_Degree	p value
RT	A>C	Cuneus.L	6.23	4.86	.010
		Cuneus.R	6.61	4.99	.003
		Inferior occipital gyrus.L	6.73	5.18	.017
		Calcarine fissure and surrounding cortex.L	6.23	5.20	.050
		Superior frontal gyrus(med).R	9.19	8.07	.030
		Superior parietal gyrus.L	6.73	5.63	.004
		Postcentral gyrus.R	7.21	5.98	.025
	C>A	Insula.L	7.40	9.99	<.001
		Insula.R	7.33	9.42	.003
		Lenticular nucleus, putamen.L	6.51	9.46	<.001
		Lenticular nucleus, putamen.R	6.66	9.28	<.001
		Lenticular nucleus, pallidum.L	6.13	8.79	.001
		Lenticular nucleus, pallidum.R	5.73	8.64	.001
		Thalamus.L	6.02	7.96	<.001
		Thalamus.R	6.06	8.14	.001
		Precuneus.L	5.50	6.71	.026
		Supramarginal gyrus.L	6.10	7.31	.018
		Rolandic operculum.L	7.60	8.53	.028
		MT	A>C	Cuneus.R	6.59
Hippocampus.R	7.35			5.36	.020
Middle temporal gyrus.L	8.41			7.38	.020
Precentral gyrus.R	8.10			6.98	.006
C>A	Insula.L		7.27	9.73	.001
	Lenticular nucleus, putamen.L		6.71	9.54	<.001
	Lenticular nucleus, putamen.R		6.35	9.05	.001
	Lenticular nucleus, pallidum.L		6.18	8.98	.004
	Lenticular nucleus, pallidum.R		5.33	8.47	.001
	Thalamus.L		6.34	8.28	.017
	Thalamus.R		6.61	8.01	.016

Regions with significant group differences in nodal degree in both task networks obtained by two sample *t* tests of AUC where curve is degree vs sparsity threshold (FDR-corrected, $p < .05$). med = medial. RT, rhyming judgment task; MT, meaning judgment task; A, adults; C, children; A_Degree, nodal degree of adults; C_Degree, nodal degree of children. L, left; R, right.

characterized by a shift from relying on subcortical-cortical and intra-subcortical connectivity to intracortical connectivity.

4.1 | Reading development is characterized by increased reliance on visual orthographic processing and decreased reliance on auditory phonological processing

There were group differences in inter-regional correlations in both tasks. In the rhyming judgment task, adults had stronger inter-regional connectivity than children between occipital and temporal visual orthographic regions, and between parietal visual spatial regions and frontal phonological processing regions. A similar pattern in the inter-regional connectivity was found in the meaning judgment task. That is, the adults had stronger inter-regional connectivity than children between occipital-temporal visual orthographic regions, as well as between temporo-parietal regions and frontal phonological processing regions. The occipito-temporal regions (e.g., fusiform gyrus, inferior and middle occipital gyri) have frequently been reported to be activated in reading tasks (Cao et al., 2010; Liu et al., 2012, 2013). These regions have been suggested to be core regions of ventral visual pathway for orthographic processing (Cao et al., 2009, 2010). The parietal regions (e.g., inferior/superior parietal lobule) have also been reported to be involved in

Chinese reading and to be core regions of dorsal visual pathway (Cao et al., 2010; Liu et al., 2009). Some researchers suggest inferior parietal lobule plays a role in phonological processing (Liu et al., 2009; Tan, Laird, Li, & Fox, 2005; Wei, Zhichao, Yanchao, & Hua, 2015), whereas superior parietal lobule seems to be involved in visual-spatial analysis (Cao et al., 2010). However, there are alternative interpretations of the role of the parietal cortex in reading. Inferior/superior parietal lobule have been suggested to be core regions of the fronto-parietal attentional network (Driscoll & Galaburda, 1991). Moreover, readers need to effectively process parafoveal information and engage eye movement mechanisms during reading (Wei et al., 2015). A recent study reported that functional connectivity strength between inferior parietal lobule and middle frontal gyrus was positively correlated with Chinese children's reading fluency, suggesting a role of inferior parietal lobule in automatized reading (Wei et al., 2015). The converging data from both tasks suggest that adults, compared to children, rely more on the connections of visual orthographic regions with frontal regions during reading. The greater reliance on the connections of visuo-orthographic and visual spatial attention regions may indicate that adult reading compared to child reading is more automated in nature.

In the rhyming judgment task, children showed stronger inter-regional correlations than adults between left superior temporal gyrus and bilateral insula, and between right Heschl's gyrus and bilateral

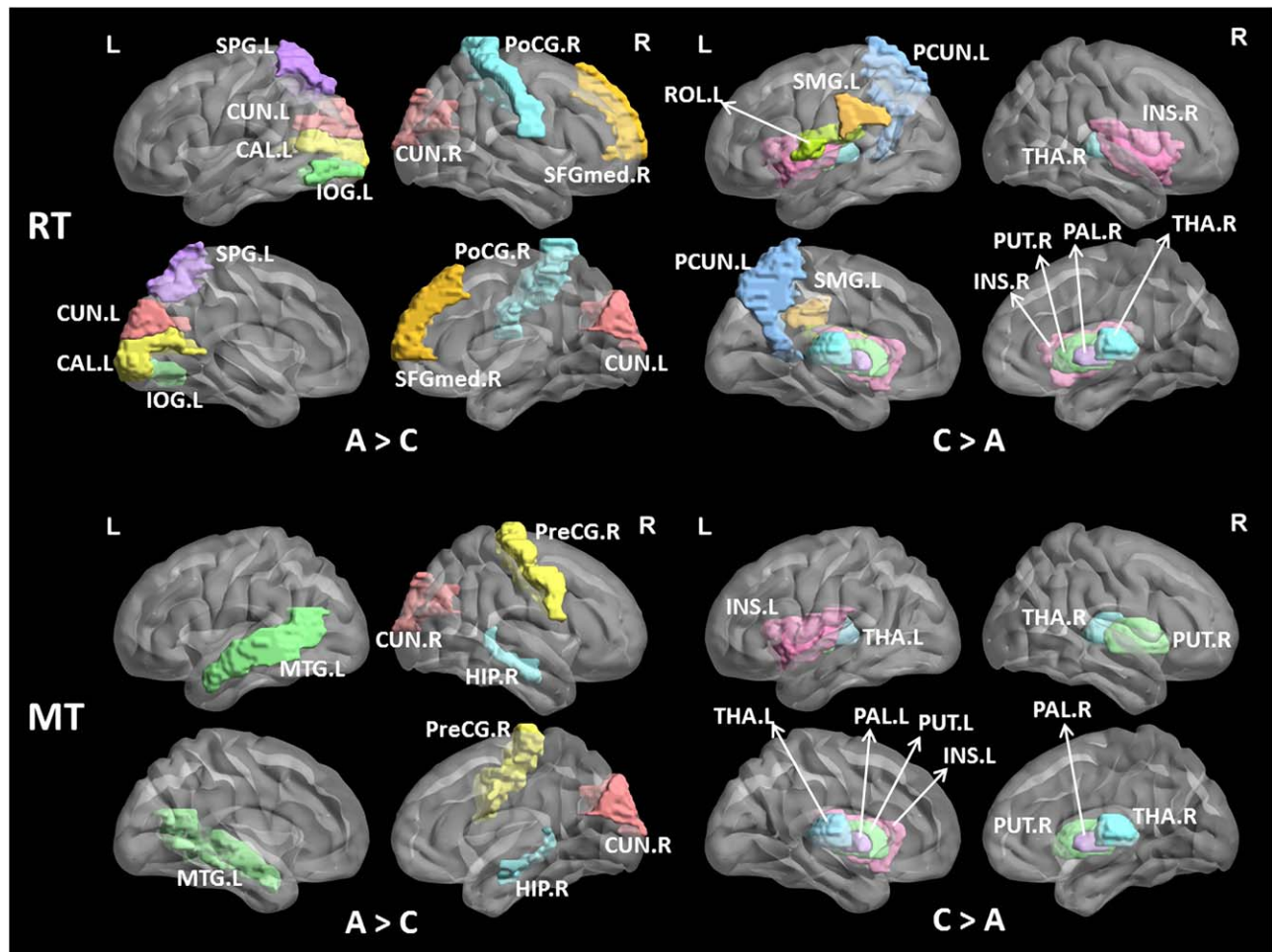


FIGURE 4 Between-group differences in nodal degree in the rhyming judgment (upper row) and meaning judgment (lower row) tasks. RT, rhyming judgment task; MT, meaning judgment task; A, adults; C, children; L, left; R, right. See Appendix table for abbreviations [Color figure can be viewed at wileyonlinelibrary.com]

rolandic operculum. Previous studies suggest that the superior temporal gyrus is an important region for phonological representations (Liu et al., 2009). Heschl's gyrus is primary auditory cortex (Altarelli et al.,

2014; Cardin et al., 2016; Warrier et al., 2009), and has often been found to be associated with acoustic analysis of speech and word identification (Warrier et al., 2009; Wong et al., 2008). The rolandic

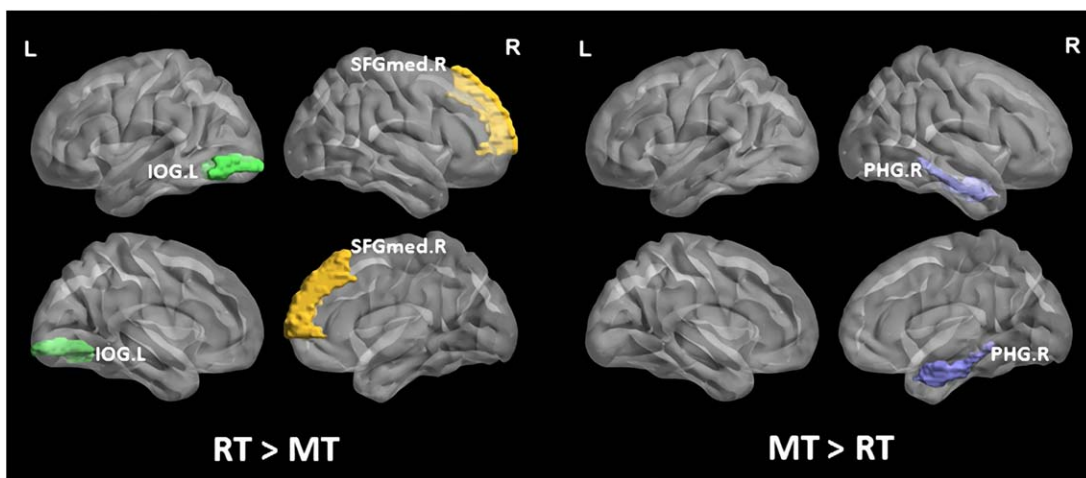


FIGURE 5 Between-task differences in nodal degree in the adult group. RT, rhyming judgment task; MT, meaning judgment task ; L, left; R, right. See Appendix table for abbreviations [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 6 Hubs in the rhyming and meaning judgment task networks

	Adult hubs	Degree	Anatomical classification	Children hubs	Degree	Anatomical classification
RT	Superior frontal gyrus(med orb).L	1.95	Prefrontal	Insula.L	2.39	Subcortical
	Superior frontal gyrus(med orb).R	2.32	Prefrontal	Insula.R	1.94	Subcortical
	Superior frontal gyrus(med).L	2.12	Prefrontal	Lenticular nucleus,putamen.L	1.97	Subcortical
	Superior frontal gyrus(med).R	2.26	Prefrontal	Lenticular nucleus,putamen.R	1.82	Subcortical
	Angular gyrus.L	1.77	Parietal	Anterior cingulate andparacingulate gyri.L	2.02	Prefrontal
	Middle temporal gyrus.L	1.70	Temporal	Anterior cingulate andparacingulate gyri.R	1.67	Prefrontal
	Middle temporal gyrus.R	1.66	Temporal			
	Anterior cingulate and paracingulate gyri.L	1.78	Prefrontal			
	Posterior cingulate gyrus.L	1.61	Parietal			
MT	Superior frontal gyrus(med orb).L	1.88	Prefrontal	Insula.L	2.34	Subcortical
	Superior frontal gyrus(med orb).R	2.04	Prefrontal	Insula.R	1.64	Subcortical
	Superior temporal gyrus.L	1.75	Temporal	Lenticular nucleus,putamen.L	2.17	Subcortical
	Superior temporal gyrus.R	1.68	Temporal	Lenticular nucleus,putamen.R	1.75	Subcortical
	Middle temporal gyrus.L	1.60	Temporal	Lenticular nucleus,pallidum.L	1.69	Subcortical
				Anterior cingulate andparacingulate gyri.L	1.58	Prefrontal
				Anterior cingulate andparacingulate gyri.R	1.61	Prefrontal

Degree refers to the normalized nodal degree, which is obtained by dividing a node's degree by the mean degree of the whole network. Degree of a node is the number of edges that connect it to the rest of the network. med orb = medial orbital. RT, rhyming judgment task; MT, meaning judgment task; L, left; R, right.

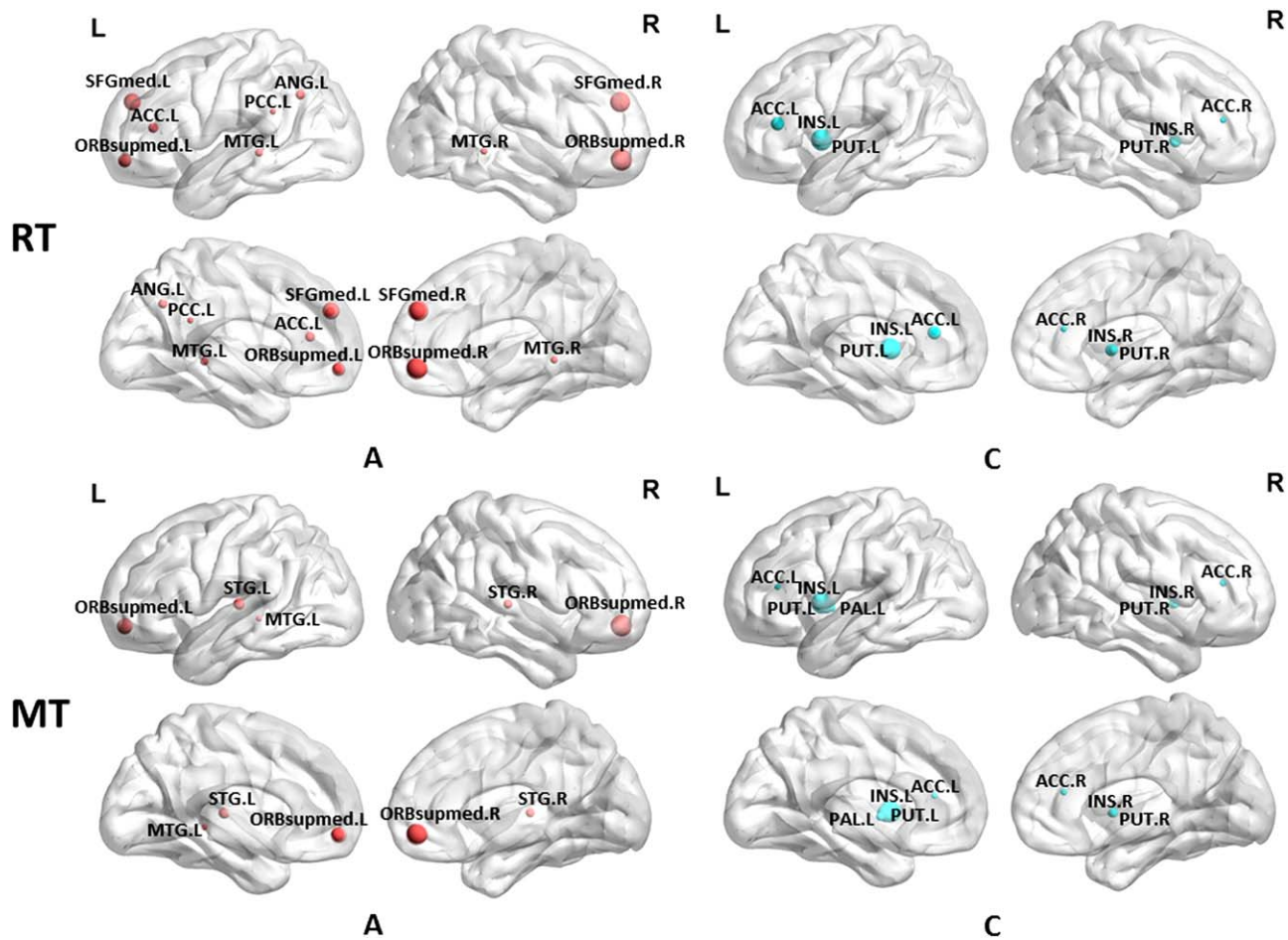


FIGURE 6 Hub distribution of the two groups in the rhyming judgment (upper row) and meaning judgment (lower row) networks. The size of nodes represents value of degree. RT, rhyming judgment task; MT, meaning judgment task; A, adults; C, children; L, left; R, right. See Appendix table for abbreviations [Color figure can be viewed at wileyonlinelibrary.com]

operculum has been suggested to be involved in the somatotopic tongue representation thus reflecting articulation (Brown et al., 2009), while the insula has been suggested to be an important region for coordinating speech articulation (Dronkers, 1996). Therefore, stronger connections between the above regions in children may indicate that children rely more than adults on connections with phonological processing and articulation-related regions in the rhyming judgment task. A similar pattern was found in the meaning judgment network. Specifically, children showed stronger inter-regional correlations between left rolandic operculum and bilateral insula. In general, we can infer that children rely more on connections with phonology and articulation-related regions during reading.

Our argument is also supported by the group differences in nodal degree in both tasks. Specifically, in the rhyming task, adults showed larger nodal degree than children in bilateral cuneus, left inferior occipital gyrus, and left calcarine fissure cortex, suggesting that adults rely more on the connections of visual processing regions with other brain regions. In the meaning judgment task, adults showed larger degree in right cuneus as well as right hippocampus and left middle temporal gyrus. The larger degree in right cuneus in adults compared to children again provides evidence for greater reliance on the connections of visual processing regions in adults compared to children. In terms of middle temporal gyrus and hippocampus, a meta-analysis of the semantic system (Binder, Desai, Graves, & Conant, 2009) has implicated that these two structures are part of the ventral semantic processing system, and may be responsible for semantic representations and semantic memory retrieval, respectively. Taken together, these findings indicate that the functional network of adult reading is characterized by greater connections with visual processing regions across both tasks.

Our study is consistent with previous developmental studies on Chinese character reading, which reported developmental increases in the activation of visual occipital regions (e.g., middle occipital gyrus) and developmental decreases in the activation of phonological processing regions (e.g., superior temporal gyrus) across multiple reading tasks (Cao et al., 2009, 2010). Here, we applied a whole-brain connectivity method and provided new evidence from a large-scale connectivity perspective for this conjecture: Chinese reading development is characterized by increased reliance on visual orthographical processing and decreased reliance on phonological processing. Of note, this developmental trend has not been reported in previous studies investigating general cognitive development using task-free resting-state data (Cao et al., 2014; Jolles et al., 2011; Supekar et al., 2009), and hence it may reflect a reading-specific developmental mechanism.

As far as we know, there is no study so far comparing adult and child reading in alphabetic languages using whole-brain large-scale functional connectivity analysis, and this makes it hard to compare our findings in logographic Chinese to those in alphabetic languages. However, there are many studies in alphabetic languages using traditional functional or effective connectivity approaches. In a resting-state fMRI study on English reading, Koyama et al. (2011) found that stronger positive functional connectivity between the left fusiform gyrus implicated in orthographic processing and inferior fronto-parietal regions implicated in phonological processing is associated with better reading

performance in adults, but not in children (Koyama et al., 2011), suggesting adults relied more on grapheme-phoneme connections for automatized reading. An effective connectivity study reported that the strength of the connections from superior temporal gyrus to inferior frontal gyrus and lateral temporal cortex decreased with age in children (ages 9–15) during a rhyming judgment task, suggesting reading development is characterized by less reliance on auditory processing regions (Bitan et al., 2007). Bitan et al. (2006) examined the effective connectivity in the same task in adult and child groups and revealed that the connectivity strength from inferior frontal gyrus to lateral temporal cortex was weaker in children compared to adults, suggesting an age-related increase in top-down modulation to phonological regions (Bitan et al., 2006). Another study examined developmental changes in effective connectivity in the same task in children (ages 9–15), and found an age-related increase in the connectivity from the left inferior frontal gyrus to the lateral temporal cortex as well as from the fusiform gyrus to the lateral temporal cortex, indicating an age-related increase in top-down and bottom-up modulation of phonological processing (Bitan, Cheon, Lu, Burman, & Booth, 2008). To sum up, it seems that both Chinese and English reading development is characterized by increased reliance on connections with orthographic regions (e.g., left fusiform gyrus) and decreased reliance on connections with auditory regions (e.g., left superior temporal gyrus). However, English reading development is additionally characterized by increased top-down modulation to phonological regions. This language difference may be due to a fact that as an alphabetic writing system with a grapheme to phoneme mapping rule, English relies more on controlled phonological processing compared to Chinese reading.

4.2 | Reading-related functional brain networks becomes more specialized over development

Greater specialization in adults is reflected in that only adults manifested between-task differences in inter-regional connectivity and nodal degree, while children did not show these differences. These findings indicate that reading development is characterized by disparate organizational patterns of inter-regional interactions for completing different tasks. Our findings support the Interactive Specialization (IS) theory, which argues that the onset of a new ability is due to changes in the interactions among several brain regions resulting in increasing specialization (Johnson, 2011). Our findings are also consistent with a previous study on Chinese reading development (Cao et al., 2009), which reported that adults showed greater activation than children in left inferior parietal lobule for the rhyming as compared with the meaning judgment task, suggesting greater specialization of phonological processing in adults.

We found that, compared with the meaning judgment task, the rhyming judgment task had greater inter-regional connectivity mainly between left parietal regions and left frontal cortex, between temporal regions and bilateral superior frontal gyri, as well as between left superior frontal gyrus and its contralateral homologous region. The inferior parietal lobule has been suggested to be involved in the conversion between orthography and phonology (Booth et al., 2002; Liu et al.,

2009). Moreover, it has been reported to be a critical region for spatial attention and play a vital role in fluent reading (Wei et al., 2015). Inferior frontal gyrus and precentral gyrus have been reported to be activated in various phonological and speech processing tasks (Cao et al., 2010; Price, 2012; Zhang, Shu, Zhou, Wang, & Li, 2010), with the former associated with phonological retrieval (Liu et al., 2009) and the latter associated with speech articulation (Fan, Mccandliss, Fossella, Flombaum, & Posner, 2005; Liu et al., 2006; Wang et al., 2016). Superior frontal gyrus is thought to be a part of cognitive execution network, involved in working memory and attention (Li et al., 2013). These stronger connections in the rhyming compared to the meaning task suggest that rhyming judgment requires stronger connectivity between phonological processing regions and higher-level cognitive control regions.

We found stronger connectivity in the meaning task than the rhyming task mainly between the orbital part of left inferior frontal gyrus and the triangular/opercular part of left inferior frontal gyrus, as well as between brain regions in the right hemisphere. The inferior frontal cortex, especially the orbital part, has been suggested to be associated with semantic retrieval (Liu, You, et al., 2013; Noppeney & Price, 2002; Rodd, Davis, & Johnsrude, 2005). Many of the stronger connections in the meaning task than the rhyming task are located in the right hemisphere. This is consistent with the argument that the right hemisphere is actively involved in lexical-semantic and context processing, with very limited phonological abilities (Vigneau et al., 2011).

As for between-task differences in nodal degree, the rhyming judgment task showed greater nodal degree in the right superior frontal gyrus and left inferior occipital gyrus; in contrast, the meaning judgment task showed greater degree in right parahippocampal gyrus. Previous studies suggested that superior frontal gyrus is involved in phonological memory retrieval (Liu, You, et al., 2013) while the inferior occipital gyrus is involved in visual orthographic processing (Cao et al., 2009, 2010). The greater nodal degree in the inferior occipital gyrus in the rhyming than semantic task may be due to the rhyming task driving the subjects to pay more attention to the phonetic radical of a character. In terms of the parahippocampal gyrus, with strong connections to the hippocampal formation, it is involved in semantic memory processing (Binder et al., 2009). These findings suggest that the rhyming judgment task relies more on the connections between regions involved in phonological memory (i.e., superior frontal gyrus) and orthographic processing (i.e., inferior occipital gyrus), while the meaning judgment task relies more on the connections of the semantic memory region (i.e., parahippocampal gyrus) with other brain regions.

4.3 | Reading development is characterized by a shift from reliance on connections of subcortical regions to reliance on connections of cortical regions

Children's reading involves multiple subcortical regions (insula, putamen, pallidum, thalamus), as shown in our results. First, the inter-regional connectivity between temporal and subcortical regions as well as between frontal and subcortical regions in children is stronger than

adults in both tasks. Second, children showed larger nodal degree in subcortical regions than adults. Last, children's hubs were mainly located in subcortical regions while adults' hubs were mainly located in cortical regions. These findings consistently suggest that children's reading relies more on subcortical regions and their connections with other subcortical and cortical brain regions. This developmental trend has been reported in previous studies on general cognitive development using task-free resting-state data (Cao et al., 2014; Jolles et al., 2011; Supekar et al., 2009), and hence it may be a domain-general developmental mechanism reflected here in reading tasks. Alternatively, these findings may indicate that domain-general developmental mechanisms are used to support reading acquisition.

It has been proposed that mature reading processes involve activation and connectivity in the "core" reading network, mainly located in cortical areas, including bilateral motor and superior temporal cortices (Turkeltaub et al., 2002), left ventral-occipitotemporal cortex including fusiform gyrus (Price, 2012; Tan et al., 2005; Turkeltaub et al., 2002), and left posterior inferior frontal cortex (Price, 2012; Tan et al., 2005). However, our findings indicate that subcortical areas, including insula and basal ganglia, such as putamen, pallidum, and thalamus may additionally be important for the reading process in children. Our results are consistent with previous evidence that subcortical regions are involved in auditory acoustic and phonological processing during reading (Booth et al., 2007; Borowsky et al., 2006; Riecker et al., 1997). Regarding the insular cortex, an fMRI study where adult participants read aloud exceptional words and pseudohomophones found the insular cortex was activated in both tasks, suggesting its role in phonological processing (Borowsky et al., 2006). A meta-analysis also confirmed the role of bilateral anterior dorsal parts of the insular in overt speech (Kurth, Zilles, Fox, Laird, & Eickhoff, 2010). Regarding the basal ganglia, Booth et al. (2007) investigated its role during a rhyming judgment task in adults and found that the putamen has unidirectional connections into both left inferior frontal gyrus and left lateral temporal cortex. They therefore argued that the putamen is engaged in cortical initiation of phonological processing (Booth, Wood, Lu, Houk, & Bitan, 2007). Further, according to a meta-analysis on basal ganglia functional connectivity, bilateral putamen significantly coactivated with subcortical (e.g., pallidum, thalamus) as well as cortical areas involved in motor and executive function, suggesting that the putamen together with other subcortical regions (e.g., pallidum and thalamus) might play an important role in motor and higher-level cognitive functions through its ample connections to cortical regions (Postuma & Dagher, 2006). Taken together, the involvement of subcortical structures (insula, putamen, pallidum, and thalamus) in children's reading may indicate that children rely on sensorimotor circuits and their connection to cortical linguistic brain regions to maintain sound representations for reading. In other words, children may rely more on phonological processing based on basic auditory processing and vocalization during the reading process. This interpretation is consistent with a previous study that found people with dyslexia exhibited hyperactivation in left subcortical regions, including caudate and thalamus during visual word rhyme judgment (Hoeft et al., 2007).

5 | LIMITATIONS

A number of caveats need to be noted regarding the present study. First, although we use methods described above to extract the time series from task trials, the signals from the task, perceptual, and null trials could not be completely separated due to the continuity of signals. However, this limitation may have minimal effects on our results, because we are mainly concerned about group and task differences in this study, and the signal-extraction method is the same between groups and tasks. Nevertheless, further research with more sophisticated signal-extraction methods would be useful for verifying our findings. Second, the sample size in this study was relatively small, thus, the generalizability of our findings may be limited. It is necessary for follow-up studies to use larger sample sizes. Third, this is a cross-sectional study, so results may be affected by intrinsic differences between subjects. Longitudinal studies are needed to better characterize the developmental differences in the functional brain network of reading. Lastly, we could not match the two age groups in Chinese reading ability due to a lack of standardized reading tests in Chinese that can be applied to both children and adults. The developmental differences found in the current study may therefore be confounded by differences in reading level between adults and children.

6 | CONCLUSION

Chinese reading development is characterized by increased reliance on the connections of visual orthographic processing regions and decreased reliance on the connections of auditory phonological representations regions. This may reflect a reading-specific developmental mechanism and supports previous literature suggesting a shift from phonological to orthographic reliance. In addition, the functional brain networks of Chinese reading tasks become more specialized over development. This is in line with the "Interactive Specialization (IS)" theory of cognitive development (Johnson, 2001, 2011). Finally, Chinese reading is characterized by more reliance on connections between cortical regions in adults compared to reliance on more subcortical-cortical and intrasubcortical connections in children. This developmental mechanism has also been reported by studies on task-free resting-state data and hence may indicate that reading development makes use of domain-general developmental mechanisms. Whether these developmental mechanisms in logographic Chinese can be generalized to alphabetic languages needs further investigation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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