



The development of brain functional connectome during text reading

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ABSTRACT

Reading is an important skill for human beings to obtain information, whose acquisition is a major learning task for children. Especially, compared with single word reading, text reading requires an integration of multiple cognitive processes, which makes its underlying neural developmental mechanism not only extremely complicated but also remained poorly understood. Employing the graph theory analysis method, the present study explored the development of brain in the context of story reading from the perspective of connectomics. Forty-two primary school students and thirty-two adults read the stories in the functional magnetic resonance imaging (fMRI) experiment. We found that compared with children, adults had increased connectivity strength, nodal degree, and modular interactions for vision-related and semantics-related brain regions while decreased connectivity strength, nodal degree, and modular interactions for phonology-related brain regions. Brain-behavior association analysis suggested that the transmission to vision-related brain circuits would enhance the reading performance in adults, whereas phonology-related brain circuits played important roles in children's reading before they develop into fluent readers. Collectively, we highlight a shift from reliance on phonology-related networks to semantics-related and vision-related networks with age for text reading, which provides insights into the underlying neural signature of developmental cognitive mechanisms.

1. Introduction

The acquisition of reading, which plays an important role for human beings to obtain information, is a major learning task for children. Nowadays, developmental neuroimaging studies provide new avenues to reveal the neural mechanism for reading acquisition. Notably, while the development of cortical organization based on word-level reading has been well explored (Cao et al., 2009, 2010, 2015; Szafarski et al., 2006; Turkeltaub et al., 2003), the investigation focusing on text reading is still in rare. That's in part because different from the word-level reading, text reading involves numerous cognitive components and their interactions, which makes the underlying neural mechanism of its development extremely complicated.

According to the seminal framework of reading systems (Perfetti and Stafura, 2014), text reading requires both processes of word decoding and reading comprehension, which includes not only linguistic processes such as orthographic, phonological, and semantic processing, but also sentence parsing (Friederici et al., 2009), inferences for bridging successive utterances (Xu et al., 2005), theory-of-mind function to

understand the writer's intentions, as well as executive functions for coordinating these processes (Ferstl et al., 2008). Consistently, the construction-integration model of reading comprehension (van Dijk and Kintsch, 1983) proposed that word decoding activates linguistic process, and then the integration process with inferencing and monitoring at the levels of the sentence, textbase, and situation model (Raudszus et al., 2019). Besides, additional processes like the eye-movement control and visual attention processes in naturalistic text reading have also been proposed (Eskenazi and Folk, 2015; Rayner, 2009).

Neurobiological findings for text reading are supportive for these models. Functional magnetic resonance imaging (fMRI) studies have showed that besides the brain regions including the left inferior frontal gyrus, left temporal-parietal cortex and left ventral occipital-temporal cortex activated by word decoding (i.e., orthographic and phonological processing) (Cattinelli et al., 2013; Price, 2012), and the left middle temporal gyrus, anterior temporal lobe, angular gyrus, posterior temporal gyrus, inferior frontal gyrus and cingulate gyrus for sentence comprehension (i.e., semantic and syntactic processing) (Friederici et al., 2009; Gold et al., 2006), the passage reading recruits extended

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language network, such as fronto- and parieto-medial brain regions for coherence; posterior middle temporal gyrus, anterior temporal lobe, medial prefrontal cortices, and dorsomedial prefrontal cortex for inference; and the dorso-lateral prefrontal cortex for executive function (Dehghani et al., 2017; Ferstl et al., 2008; Xu et al., 2005; Yarkoni et al., 2008).

Developmentally, overt reading precedes covert reading (Laubrock and Kliegl, 2015). Behavioral studies found that beginning readers of either English or Chinese rely more on phonology during silent sentence reading (e.g., Coltheart et al., 1990; Zhou et al., 2018). Meanwhile, skilled adult readers shift from encoding the exact words to semantic processing, including representing and explaining the ideas conveyed in the text (Kintsch and van Dijk, 1978; Kuperman et al., 2018). fMRI studies using word-based rhyming tasks found a larger activation in the left superior temporal gyrus for children than adults, indicating a reduced reliance on phonology with the development of reading skill in both English (e.g., Booth et al., 2003, 2004) and Chinese readers (e.g., Cao et al., 2009).

Notably, traditional activation algorithm with task fMRI can reveal the involved regions during cognitive processing but not the underlying information transmission circuits, which makes it insufficient to reveal the neurodevelopmental mechanism for text reading. Recently, brain connectomics, which organizes the whole human brain into a complex network through non-invasively mapping structural and functional connectivity patterns (Bullmore and Sporns, 2009, 2012), provides a new avenue to reveal the complete picture of brain information transformation. Studies using resting-state (Vogel et al., 2012; Koyama et al., 2011) and word-level reading task fMRI data (Bitan, 2005) have reported weaker brain connections between reading-related regions in children compared to adults. Interestingly, Liu et al. (2017) found that during word reading task, the interregional connectivity increased in occipital regions but decreased in temporal regions with development. However, the exploration of the development of whole-brain functional networks for text-reading tasks is still in lack.

Here, employing the graph theory analysis method, we aim to reveal the development of brain functional connectome in the context of story reading. Regional, connectional and modular properties were compared between the whole-brain networks of children and adults during performing a text reading task. Besides, we analyzed the neural association between age and behavior performance by measuring the correlation between brain network measurements with reading score and group/age effects. On the basis of previous studies, we expected that children would more rely on brain systems for word decoding especially phonological processing, whereas adults would exhibit more mature brain function for unique processes in text reading such as higher-level semantic processing for inference and interpretation as well as visual attention. Besides, these neural changes contribute to the improvement in behavior performance with development.

2. Methods

2.1. Subjects

Forty-two children (age: 10.3 years \pm 0.08 years; 22 females) and thirty-two adults (age: 23.8 \pm 4.6 years; 18 females) participated in the experiment (See Table 1 for more details on demographics and

Table 1
Demographic and behavioral information for the children and adults.

	Children	Adults	P values
N	42	32	-
Age (years)	10.3 \pm 0.8	23.8 \pm 4.6	<. 001
Male n (%)	22 (52.4)	14 (43.8)	.542
Reaction time (ms)	2201 \pm 449	1947 \pm 449	.019
Accuracy	0.88 \pm 0.14	0.95 \pm 0.08	.013

behavioral performances). Children were fourth to sixth graders students recruited from primary schools in Beijing and Shandong. Adults were recruited from universities in Beijing. All participants were native speakers of Mandarin Chinese with normal or corrected-to-normal vision and right-handed. This study was approved by the Research Ethics Committee at Capital Normal University. All subjects signed an informed written consent form before the experiment. None of them had a history of either neurological diseases or psychiatric disorders according to their self-reports.

2.2. Experimental procedure

Four brief introductions of Hans Christian Andersen's fairytale stories in a Chinese extracurricular book were edited as the materials for the reading task (Zhou et al., 2020). Each story was presented in one block with 10 sentence trials. Each sentence had an average of 13.6 (SD = 1.5) characters (see Fig. 1). All the characters in the stories have been listed as learning materials in textbooks from Grades 1–4. Each sentence was presented for 3500 ms, followed by a blank screen for 500 ms. Each character was presented in Song font and occupied a 48 \times 48 pixel grid with one character equal to approximately one degree of visual angle. Subjects were told to silently read the story and then judge the correctness of two comprehension questions by pressing a button with their right hand as accurately and fast as possible after each story. Each question was presented for 5000 ms, followed by a blank screen for 1000 ms. The task started with 14 s of rest, and each block was followed by 14 s of rest. During the rest periods, there was a fixation presented at the center of the screen, and the participants were asked to look at it. All subjects practiced by reading two different stories and answering the questions outside the scanner before the experiment.

2.3. Image acquisition

All MRI data were obtained on a SIEMENS PRISMA 3-Tesla scanner in the Imaging Center for Brain Research at Peking University. A total of 139 whole brain EPI volumes were acquired with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 90°, in-plane imaging resolution = 3.5 \times 3.5 mm², FOV = 224 \times 224 mm², slice thickness = 3.5 mm with no gap, slice number = 33. A co-registered T₁-weighted images were acquired with MP-RAGE sequence with the following parameters: TR = 2530 ms, TE = 2.98 ms, in-plane imaging resolution = 0.5



Fig. 1. The procedure for a task block and an example of the material. The English translations were presented under each trial.

× 0.5 mm², FOV = 256 × 224 mm², slice thickness = 1 mm with no gap, sagittal slice number = 192, thickness = 3.5 mm. The acquired T1-weighted image was zero-filled to 256 × 224 image matrix.

2.4. Preprocessing

As the current study focused on the functional connectivity of task-based fMRI, we concatenated the timecourses of task blocks to construct the FC matrix for network analysis (Richiardi et al., 2011). Image preprocessing was performed with DPABI (Yan and Zang, 2010) with the following steps: slice timing, realigning, normalizing to MNI space by using DARTEL segmentation (resampling to 3 × 3 × 3 mm³), spatial smoothing by DARTEL with a 6-mm FWHM Gaussian kernel, removing linear trends, high-pass temporal filtering with a cutoff of 0.01 Hz, and regressing out potential nuisance variables including 6 head motion parameters and the averaged signal from white matter, cerebrospinal fluid tissue and the whole brain. The data of 3 children other than that of 42 participants were excluded from analysis due to either head motion displacements > 3 mm or rotation > 3°.

2.5. Network analysis

The automated anatomical labeling (AAL) parcellation was used for whole-brain partitioning to define the nodes in the brain networks (Tzourio-Mazoyer et al., 2002). For each subject, the time series of each node during the text reading task were calculated by averaging the time series of all voxels within the region. Edges were calculated using the Pearson correlation coefficient between the time courses for each pair of nodes. Due to the ambiguous biological explanation of negative correlations (Fox et al., 2009; Murphy et al., 2009), only positive correlations were retained for further network analyses.

First, we explored the developmental effects on functional connectivity strength. Before the group comparisons, a one-sample *t*-test was conducted in each group on the Fisher-*z*-transformed Pearson correlation coefficients for the connectivity between all pairs of brain regions. Connections that showed significant results in at least one group (*p* < 0.05 with FDR correction) were used for subsequent group comparison.

To further explore the development of brain network topological properties, we constructed the binarized functional brain network for each subject through thresholding the correlation matrices with a set of sparsity thresholds (ranging from 0.05 to 0.5 with a step of 0.05). The mean values of all explored network properties across the sparsity range were used for group comparisons. We explored the developmental effects on nodal and modular properties of the whole-brain network during text reading. The graph theoretical analysis was conducted with GREYNET (http://www.nitrc.org/projects/gretna/) (Wang et al., 2015). Nodal degree is defined as the summed number of edges that connect a given node to the remaining regions, which reveals the importance of the node in the network. For modular analysis, we employed a pre-defined cognitive components template for the modular analysis which was adapted from Yeo et al. (2015) and generated based on a meta-analysis of task data with 12 cognitive components. M1 to M12 were labelled according to the top tasks for each cognitive component (see Table 2). Brain nodes were grouped to modules according to the template. The intra- and inter-module connectivity were calculated as the summed number of connections within and between-modules and

then compared between groups.

2.6. Statistical analysis

2.6.1. Identifying the developmental effects on network properties

We explored the developmental effects on connectional, nodal, and modular metrics using two-sample *t*-tests with sex and head motion (i.e., root mean square for six head motion parameters, $\sqrt{(Tx^2 + Ty^2 + Tz^2 + Rx^2 + Ry^2 + Rz^2)}$) as covariates. FDR corrections were conducted for multiple comparisons. The results were visualized with BrainNet Viewer (Xia et al., 2013).

2.6.2. Brain-behavior association analysis

2.6.2.1. Correlation analysis. To determine the relationship between brain functional network measurements and task performance, we firstly conducted a correlation analysis between each metrics and behavior performance with head motion and sex controlled. For each subject, the behavior performance during reading comprehension task was scaled as the reading score through dividing the accuracy by reaction time. As a result, higher score indicated better reading performance by taking account of both speed and accuracy. For each brain network metric showing significant group differences, we conducted the correlation analysis between the identified metric and the reading score in each group separately.

2.6.2.2. Mediation analysis. For the brain network metrics showing significant association with the reading score, we assessed whether they mediated the association between the age group and the behavior performance. In order to test the significance of mediation effects, bias-corrected bootstrapping was performed (McCartney et al., 2006). This method directly produces confidence intervals from percentiles. In this study, we chose 95 % confidence intervals. The independent (predictor) and dependent (predicted) variables were the age group and the reading score, respectively. The proposed mediator was the metrics associated with reading score.

2.6.2.3. Pattern similarity analysis. We conducted an association analysis between the over-all spatial pattern similarity of all network metric (i.e., functional connectivity strength, nodal degree, within-modular interactions, and between-modular interactions) and behavior performance. For each group, we first calculated the averaged spatial pattern of every network metric across all subjects. Then, the spatial pattern-similarity between each subject and the group-averaged one were computed through the Pearson correlation coefficients. Finally, we computed the relationship between the Fisher-*r*-to-*z* transformed correlation values and the task performance in each group respectively.

2.6.2.4. Validation analysis. In order to further exclude the effect of head motion, we conducted the scrubbing analysis to remove time points with large head motion under frame-wise displacement threshold of 0.5 mm (Power et al., 2012).

Table 2

The functions for 12 cognitive modules.

	M1	M2	M3	M4	M5	M6
Function Label	Motor task	Overt reading task	Auditory/phonological task	Visual task	Covert reading/semantic task	Saccade/visual attention task
Function Label	M7	M8	M9	M10	M11	M12
Function Label	Sensory task	Flanker/executive functioning task	N-back/working memory task	Theory of mind task	Emotion task	Reward task

3. Results

3.1. Behavioral performances

The comprehension questions were served to examine whether the participants completed the task seriously and their reading capacity. The average accuracies on the comprehension questions for adults and children were 95% (SD = 7%) and 88% (SD = 14%) (The possible maximum for accuracy was 8 items) respectively. The average reaction times for the comprehension questions for adults and children were 1947 ms (SD = 449 ms) and 2229 ms (SD = 450 ms) respectively. There were significant group differences in accuracy, reaction time, and the reading score through dividing the accuracy by reaction time ($p < 0.05$).

3.2. Development of functional connectivity strength

Compared with children, the adults exhibited significantly stronger functional connections between anterior and posterior cingulate cortices and orbital frontal areas within both hemispheres ($p < 0.01$, FDR correction). In the left hemisphere, the adults had stronger functional connections between the frontal areas with the angular gyrus, middle temporal gyrus, and rectus cortex, between the fusiform gyrus with the inferior occipital cortex, between the lingual gyrus with calcarine, and between the olfactory with the temporal pole ($p < 0.01$, FDR correction). In the right hemisphere, the adults had stronger functional correlations between the olfactory cortex and the superior temporal gyrus and between the supplementary motor area with the putamen ($p < 0.01$, FDR correction). In the contrast, the children showed significantly stronger functional connections among the frontal cortices (e.g., the opercular part of inferior frontal gyrus), temporal cortices (e.g., Heschl cortex and superior temporal gyrus), and subcortical regions (e.g., insula and putamen) within both hemispheres than the adults ($p < 0.01$, FDR correction). Overall, the adults had more intra-hemispheric connections linking the anterior frontal regions and the posterior temporal regions mostly in the left hemispheric, while the children recruited more inter-hemispheric connections linking bilateral auditory-related and subcortical regions. Fig. 2 and Table 3 demonstrate the detailed results of the group effects on functional connectivity strength.

3.3. Development of nodal degree

The between-group differences in nodal degree during story reading were shown in Table 4 and Fig. 3. The group of adults had a significantly higher nodal degree in the left superior occipital cortex, left middle occipital cortex, left cuneus, and bilateral cingulum cortices (posterior part) than the children ($p < 0.05$, FDR correction). Meanwhile, the children showed significantly higher nodal degree in bilateral inferior frontal gyri (opercular part), bilateral insula, bilateral caudate, bilateral putamen, bilateral pallidum, and right thalamus ($p < 0.05$, FDR correction).

3.4. Development of modular structure

The group mean functional correlation matrices ordered by modules for the adults and children were presented in Fig. 4. We labelled the functions of M1 to M12 according to the top tasks for each cognitive component in Yeo et al. (2015) (see Table 2 and Fig. 4). Regarding to the within-modular connections, the adults had more connections within the M5 network (covert reading/semantic task) and M6 network (saccade/visual attention task), while fewer connections within the M7 network (sensory task) than the children ($p < 0.05$, FDR corrected). Regarding the intra-modular connections, the children had more connections of M3 (auditory/phonological task) – M9 (N-back/working memory task), M3 (auditory/phonological task) – M5 (covert reading/semantic task), M5 (covert reading/semantic task) – M7 (sensory task), M7 (sensory task) – M8 (Flanker/executive functioning task), and M8 (Flanker/executive functioning task) – M9 (N-back/working memory task) than the adults ($p < 0.05$, FDR corrected). The adults had more intra-modular connections of M1 (motor task) – M6 (saccade/visual attention task) and M8 (Flanker/executive functioning task) – M10 (theory of mind task) than the children ($p < 0.05$, FDR corrected).

3.5. Brain-behavior association analysis

3.5.1. Correlation between brain network metrics and task performance

We found that in the group of adults, there were significantly positive correlations between the reading score and the nodal degree of the left middle occipital cortex (Fig. 5A, $r_p = 0.52$, $p = 0.003$). Meanwhile, in the group of children, we detected significantly negative correlations

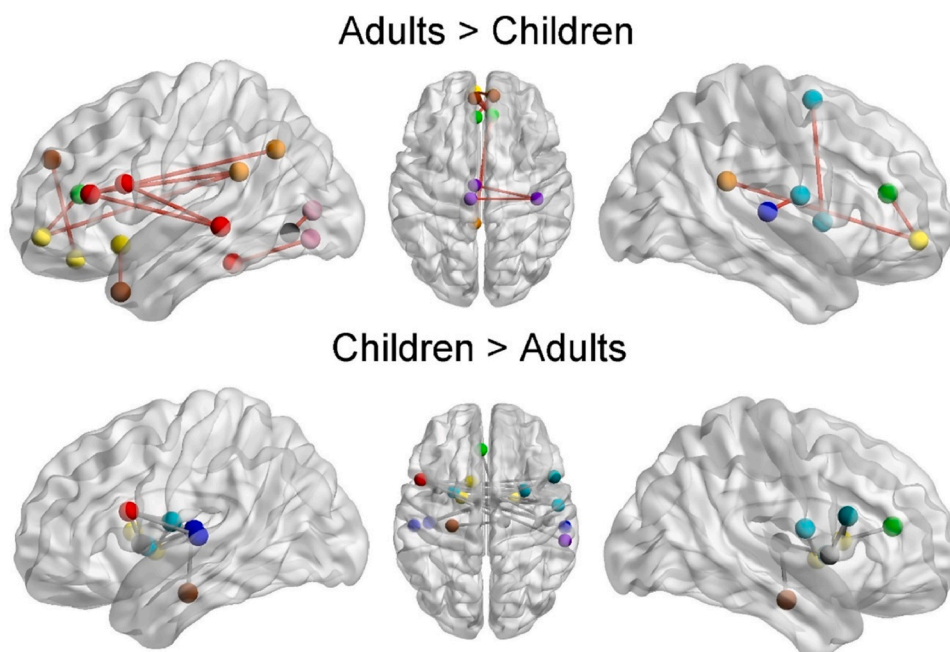


Fig. 2. Group differences in functional connectivity between the adults and children. The top row indicates stronger functional connections in the adults. The bottom row indicates stronger functional connections in the children. The colors of the nodes indicate the cognitive component to which each region belonged according to Yeo et al. (2015): purple (M1), cyan (M2), blue (M3), pink (M4), red (M5), gray (M7), light green (M8), dark green (M9), orange (M10), brown (M11), and yellow (M12). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 3
Group differences in interregional connections.

	Within LH		Within RH		Between LH and RH	
Adults > Children	IFG _{Oper}	IFG _{Tri}	MedFG _{Orb}	CING _{Ant}	CING _{Ant}	MedFG _{Orb}
	IFG _{Oper}	MTG	MedFG _{Orb}	CING _{Post}	CING _{Mid}	PostCG
	IFG _{Tri}	AG	ROL _{Oper}	STG	CING _{Post}	MedFG _{Orb}
	IFG _{Tri}	MTG	SMA	PUT	CING _{Post}	CING _{Ant}
	CING _{Ant}	CING _{Post}			MedFG _{Orb}	CING _{Ant}
	MedFG _{Orb}	CING _{Ant}			MedFG _{Orb}	SFG _{Med}
	MedFG _{Orb}	CING _{Post}			PCL	PostCG
	SFG _{Med}	REC			REC	SFG _{Med}
	IOC	FG				
	LING	CAL				
	OLF	TP _{Mid}				
		ROL _{Oper}	IFG _{Oper}	INS	IFG _{Oper}	ROL _{Oper}
	Children > Adults	IFG _{Oper}	INS	IFG _{Oper}	CAU	IFG _{Oper}
IFG _{Oper}		HG	ROL _{Oper}	PAL	IFG _{Oper}	SMG
IFG _{Oper}		STG	INS	CAU	INS	CAU
ROL _{Oper}		PAL	INS	PUT	INS	PUT
INS		CAU	INS	PAL	INS	PAL
INS		PUT	CING _{Ant}	CAU	INS	THA
INS		PAL	INS	THA	CING _{Ant}	THA
PHG		THA	PHG	THA	HIP	THA
PUT		HG			CAU	HG
PAL		HG			PAL	HG
PAL		STG			PAL	STG
					INS	IFG _{Oper}
					HG	IFG _{Oper}
				PAL	ROL _{Oper}	
				PUT	INS	
				PAL	INS	
				STG	PAL	

Note. L = left, R = right. AG = angular gyrus, CAL = calcarine; CAU = caudate, CING = cingulum gyrus, FG = fusiform gyrus, HG = Heschl gyrus, HIP = hippocampus, IFG = inferior frontal gyrus, INS = insula, IOC = inferior occipital cortex, LING = lingual gyrus, MedFG = medial frontal gyrus, MTG = middle temporal gyrus, OLF = olfactory, PAL = pallidum, PCL = paracentral lobule, PHG = parahippocampal gyrus, PostCG = postcentral gyrus, PUT = putamen, REC = rectus, ROL = Rolandic cortex, SFG = superior frontal gyrus, SMA = supplementary motor area, SMG = supramarginal gyrus, STG = superior temporal gyrus, THA = thalamus, TP = temporal pole. Ant = anterior, Med = medial, Mid = middle, Oper = the opercular part, Orb = the orbital part. Post = posterior.

Table 4
Group differences in nodal degree.

Contrasts	ID	Regions	Mean degree values in adults	Mean degree values in children	P
Adults > Children	1	L. CINGpost	11.75	9.59	<0.001
	2	R. CINGpost	11.13	9.42	0.001
	3	L.CUN	9.33	8.17	0.002
	4	L.MOC	9.64	8.53	0.004
	5	L.SOC	8.94	7.94	0.005
	6	L.CAU	10.16	11.94	0.001
Children > Adults	7	R.CAU	10.51	12.35	<0.001
	8	L.IFGoper	12.33	14.62	<0.001
	9	R.IFGoper	12.58	14.50	<0.001
	10	L.INS	10.76	13.55	<0.001
	11	R.INS	10.86	13.67	<0.001
	12	L.PAL	12.60	15.19	<0.001
	13	R.PAL	13.03	15.21	<0.001
	14	L.PUT	10.86	13.91	<0.001
	15	R.PUT	11.27	13.93	<0.001
	16	L.THA	12.66	13.87	0.012

Note. L = left, R = right. CAU = caudate, CING = cingulum gyrus, CUN = cuneus, IFG = inferior frontal gyrus, INS = insula, MOC = middle occipital cortex, PAL = pallidum, PUT = putamen, SOC = superior occipital cortex, THA = thalamus. Post = the posterior part, Oper = the opercular part.

between the reading score and the modular interaction of M3 (auditory/phonological task) with M9 (N-back/working memory task) (Fig. 5B, $r_p = -0.36, p = 0.022$).

3.5.2. Mediation analysis

In order to investigate the relationships among age group, brain

indicators and reading performance, we applied mediation analyses by taking the age group, brain indicators (the nodal degree of the left middle occipital cortex or the modular interaction between M3 and M9) and reading performance as the predictor, mediator, and outcome, respectively. When the nodal degree of the left middle occipital cortex was entered into analysis, the standardized parameter estimates for the age group effect on reading performance reduced from .087 ($p = .009$) to .065 ($p = .059$), indicating a complete mediation effect of the nodal degree of the left middle occipital cortex (Fig. 5D). To test the significance of the indirect effects, bootstrapping procedures were used (McCartney et al., 2006). This provided 95 % confidence intervals (sum of the two indirect effects in each model, corrected for bias) for the mediation model (LLCI-ULCI: 0.0007–0.0692). As this interval does not include zero, it indicates a significant mediation effect. There was no significant mediation effect of the modular interaction between M3 and M9.

3.5.3. Correlation between pattern-similarity and task performance

We found that adult individuals with higher overall spatial pattern similarity in functional connectivity strength to children would have worse reading performance ($r_p = -0.37, p = 0.044, \text{Fig. 5C}$).

3.6. Validation analysis

We found that the head motion of children was significant larger than that of adults ($t = -3.089, p = 0.003$). To exclude this effect, we have included head motion as a co-variate in the above analyses. In order to further validate our results, we conducted the scrubbing analysis to remove time points with large head motion. The group effect on FC strength after scrubbing remained the similar pattern with that before scrubbing (i.e., 87 % retention of FCs with group difference). Specifically, 3 out of 20 FCs (i.e., between the opercular part of left

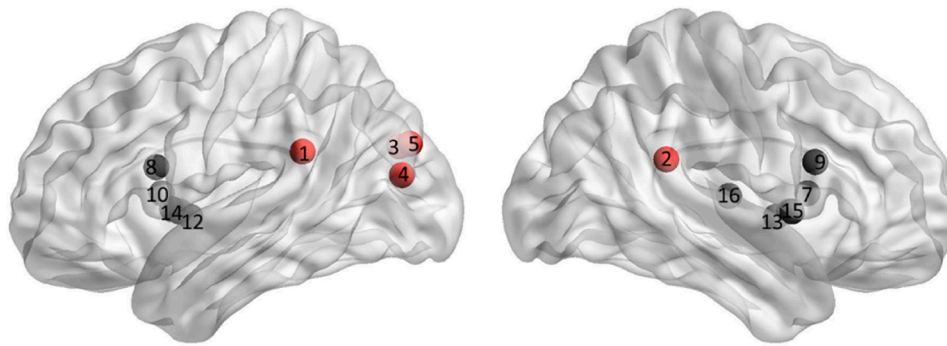


Fig. 3. Group differences in nodal degree. Spheres are drawn on center coordinates of AAL regions that showed significant group differences in nodal degree. Red spheres indicate a larger nodal degree in adults than children. Gray spheres indicate a larger nodal degree in children than adults. The label for each region can be found in Table 4 (ID) according to the numbers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

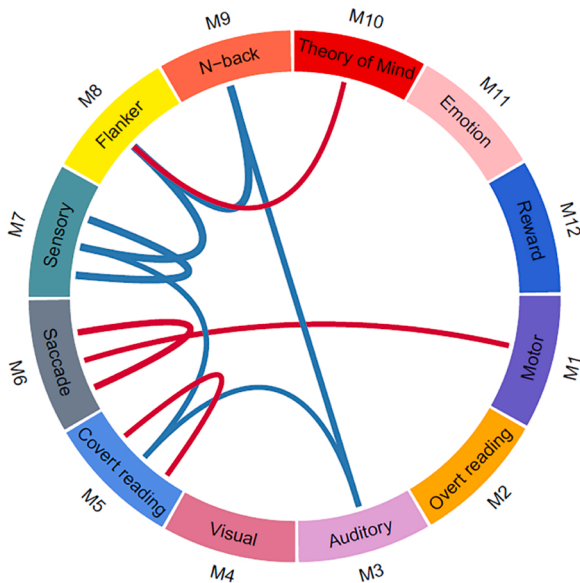


Fig. 4. Differences in connections within and between modules. The red lines indicate more edges within or between modules in adults than children. The blue lines indicate more edges within or between modules in children than adults. All effects were corrected with FDR method at $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

inferior frontal gyrus and left middle temporal gyrus, left medial superior frontal gyrus and right rectus, left fusiform and left inferior occipital cortex), which showed stronger connectivity strength in adults, disappeared after scrubbing. 5 out of 39 FCs (i.e., from the opercular part of right inferior frontal gyrus to right caudate, insula, and Heschl gyrus, between left hippocampus and right thalamus, left caudate and right Heschl gyrus), which showed stronger connectivity strength in children, disappeared after scrubbing. An additional region (i.e., the right Rectus) showed larger nodal degree in adults relative to children after scrubbing. The group effect on modular interaction was also remained as the main results after scrubbing.

4. Discussion

In this study, we used graph theoretical analysis to investigate the neural development of text reading through examining the group differences in functional connectivity, nodal degree, and modular structure and their associations with behavior performance. Our findings showed that compared with children, adults had increased connectivity strength, nodal degree, and modular interactions for vision-related and semantics-related brain regions while decreased connectivity strength, nodal degree, and modular interactions for phonology-related brain

regions. In addition, we observed increased connections of the theory of mind (i.e., extended semantics) and saccade (i.e., visual attention) networks in adults and more engagement of phonologic neural pathway and its communication with executive function and memory networks in children, which might be a unique developmental landmark for text reading compared with word reading. Brain-behavior association analysis indicated that the transmission to vision-related brain circuits would enhance the reading performance in adults, whereas phonology-related brain circuits played important roles in children's reading before they develop into fluent readers. In addition, adults with the poorest language comprehension performance seemed not to fully engage normal semantic processing pathways but instead engaged phonologic pathways like children during the task.

Developmentally, reading aloud precedes silent reading (Laubrock and Kliegl, 2015), which leads to the conclusion that beginning readers rely more on phonological information. Previous behavioral studies (e.g., Coltheart et al., 1990; Zhou et al., 2018) have found that beginning readers of both English and Chinese rely more on phonology during sentence reading than adult readers. In this study, we found that the children recruited more functional connectivity linking the modules (e.g., M3 and M7) and regions (e.g., inferior frontal gyrus, superior temporal gyrus, supramarginal gyrus, insula, and thalamus) associated with phonological processing. We found that children had more connections within the M7 (sensory task), which including the supramarginal gyrus and insula. These two regions are typically somatomotor- and phonology-related areas according to previous research (Booth et al., 2006; McDermott et al., 2003; Mohr et al., 1978; Price and Mechelli, 2005; Riecker et al., 2000). We also detected stronger connectivity of the left superior temporal areas and the opercular part of the inferior frontal gyrus in children, which have been consistently found important for mapping orthography to phonology (Jobard et al., 2003). Besides, the subcortical areas, including thalamus, pallidum and putamen, have also been reported involved in auditory-motor processing (Booth et al., 2007; Liu et al., 2017; Postuma and Dagher, 2006). The study of Liu et al. (2017) using the rhyming judgment task of Chinese characters have showed that children exhibited stronger interregional correlations between the left superior temporal gyrus with bilateral insula and between the right Heschl gyrus with bilateral Rolandic operculum compared with adults. In this study, we additionally found that children relied more on the interactions between phonology-related systems (M3 and M7) with other networks serving for working memory (M9), executive function (M8), and covert reading (M5), which might compensate for relatively non-automatic reading skills. It is relevant that the dorsolateral prefrontal cortex, which is associated with working memory and executive function, has been found to increase with task demands (correspond to low automaticity) in text reading (Ferstl et al., 2008). It seems likely that children may not be able to develop into fluent readers without first using a phonology based representation that then, with practice, develops into more automatic processing.

Interestingly, we found that the children had more evident intra-hemisphere connections, especially for the bilateral phonological

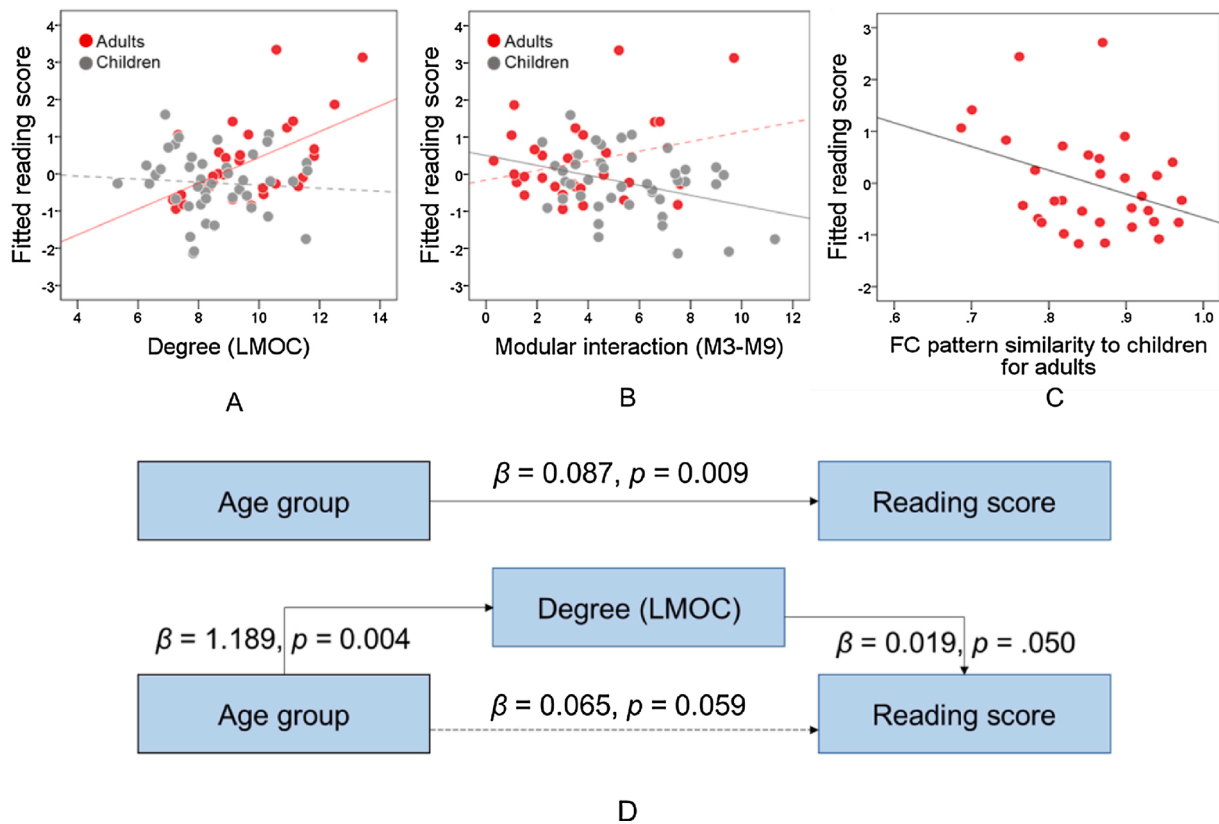


Fig. 5. Scatter plots for brain-behavior relationships. A. The scatter plot between the fitted reading score (the fitted value of the linear regression model with reading score as the dependent variable and with sex and head motion as covariates) and the nodal degree of the left middle occipital cortex. B. The scatter plot between the fitted reading score with the modular interaction of M3 (auditory/phonological task) - M9 (N-back/working memory task). LMOC = left middle occipital cortex. C. The scatter plot between the fitted reading score and FC spatial pattern similarity to children for adults. D. The mediation implemented by nodal degree of LMOC from the age group on reading performance.

regions. This is consistent with the study of [Zhong et al. \(2016\)](#) which found that adults exhibited more left-lateral asymmetry mainly around the parasyllian area, posterior tempoparietal cortex, and fusiform gyrus than adolescents. Previous studies ([Illingworth and Bishop, 2009](#); [Shaywitz et al., 1998](#)) also reported that dyslexic adults and children have atypical bilateral symmetry relative to the left-hemisphere lateralization observed in controls. Again, these results highlighted children's reliance on phonological processing during reading. Notably, we also observed two stronger connections between phonology-related regions in the adults. Here, the right superior temporal gyrus has been related to tone and prosodic processing ([Zhang et al., 2010](#)), which may be still immature in children.

Besides, we found that adults rely more on vision-related regions than children. We detected stronger functional connectivity linking the fusiform gyrus and inferior occipital cortex, and higher nodal degree of the inferior occipital cortex and superior occipital cortex in adults than children, which were consistent with previous findings in single-word reading task ([Cao et al., 2010](#); [Liu et al., 2017](#)) and resting-state fMRI studies ([Vogel et al., 2012](#)). [Finn et al. \(2014\)](#) found that children with dyslexia have disconnections among vision-relation regions relative to typical controls, which also supporting the important role of these regions for reading. Besides, we found that adults exhibited more connections within M6 (saccade/visual attention task) and between visual-motor-related modules (M6 and M1) compared with the children, highlighting the requirements of more eye-movement controlling and parafovea processing for adults. This system is situated in the dorsal visual path way and plays an important role in naturalistic text reading ([Zhou et al., 2019](#)).

Moreover, the present study highlighted the development of complex semantic system for text reading. Specifically, we found that regions in

M5, M10, M11, and M12 (e.g., inferior frontal gyrus, middle temporal gyrus, superior frontal gyrus, medial frontal gyrus, angular gyrus, cingulate gyrus, and temporal pole) showed stronger functional connectivity and modular interactions in adults compared with children. The regions in M5 component (e.g., the left inferior frontal gyrus and middle temporal gyrus) were reported serving for basic semantic processing ([Friederici, 2011](#)). The medial frontal gyrus (in M12) and the posterior part of the cingulate gyrus (in M10) have been reported additionally active in comprehensible text processing compared with incoherent language (i.e., word lists or unrelated sentences) ([Ferstl et al., 2008](#)). M10 for the theory-of-mind serves to inference the writer's intentions ([Ferstl et al., 2008](#)). Besides, M11 and M12 for emotion and rewarding serve to inference the writer's emotion according to semantics and prior knowledge ([Hsu et al., 2015](#)). Our results jointly indicate that adults have a relatively mature and deep-level semantic processing for text reading compared with children. The increased interaction between M8 (Flanker/working memory task) and M10 (theory of mind) in adults also likely reflects their improvements in executive functioning and deep-level semantic processing other than basic reading-related factors. These findings provide unique insights of the neural mechanisms for narrative story reading and are consistent with previous models ([Perfetti and Stafura, 2014](#); [Raudszus et al., 2019](#); [van Dijk and Kintsch, 1983](#)).

Notably, through the brain-behavior association analysis, we found a significant positive correlation between the nodal degree of the left middle occipital gyrus and reading performance, which suggests that the more engagement of vision-related brain circuits for adults would enhance the reading performance. The results of mediation analysis further highlighted the critical role of vision-related brain circuits for the development of reading skill. In contrast, the negative correlation

between the modular interaction of M3-M9 and reading performance in children might indicate the compensating roles of the engagement of phonology-related brain circuits for poorer reading performance. The result of mediation analysis validated the critical role of the identified brain functional connectome measurement, the nodal degree of the left middle occipital gyrus, in the development of text reading skill. Besides, the more adults are children alike in whole-brain functional connectivity patterns, the poorer their reading performance would be.

The present study only used the on-line reading score as the indicator of reading performance, and there were no age-based norms to generate a standardized score for analysis. Brain-behavior analysis based on tests for multifaceted reading skills will consolidate our findings. In addition, the use of standardized reading scores based on age-based norms will help to examine whether child and adult samples have equivalent reading competency among peers (e.g., both group had typically developing reading levels), which can be considered in future studies.

Taken together, the present study has shown that during text reading, children rely more on the coordination of phonology-based perceptual system and other systems (e.g., executive and working memory systems), while adults rely more on the internal consistency of covert reading, semantic and visual systems. And these general trends in subjects' brain functional networks were significantly correlated with their reading capacity.

Data availability statement

The data supporting the current study have not been deposited in a public repository due to the restrictions on public sharing of the participants' data but are available on request.

Declaration of Competing Interest

The authors declare no competing financial interests.

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