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Abstract

Building robust letter-to-sound correspondences is a prerequisite for reading, and such audiovisual integration becomes progressively automatic with development. However, the neural mechanisms underlying the development of audiovisual integration for reading are largely unknown. This study used functional magnetic resonance imaging (fMRI) in a lexical decision task to investigate the changes of brain functional networks that support audiovisual integration for reading between normally developing children (9-12 years old) and adults (20-28 years old). The identified networks were further examined in children with developmental dyslexia (9-12 years old). Results revealed that adults enhanced connectivity in a prefrontal-superior temporal network relative to children, reflecting the attentional modulation to the development of audiovisual integration. Moreover, this network was disrupted in dyslexics, confirming its essential role in audiovisual integration for reading. This study, for the first time, elucidates the neural basis underlying the development of audiovisual integration for reading.

Full Text

Preamble

Brain Networks Underlying the Differences in Audiovisual Integration for Reading Between Children and Adults and Its Disruption in Dyslexia

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Abstract

Establishing robust letter-to-sound correspondences is a prerequisite for reading, and such audiovisual integration becomes progressively automatic with development. However, the neural mechanisms underlying the development of audiovisual integration for reading remain largely unknown. This study used functional magnetic resonance imaging (fMRI) during a lexical decision task to investigate changes in brain functional networks that support audiovisual integration for reading between normally developing children (9–12 years old) and adults (20-28 years old). The identified networks were further examined in children with developmental dyslexia (9–12 years old). Results revealed that adults showed enhanced connectivity in a prefrontal-superior temporal network relative to children, reflecting attentional modulation in the development of audiovisual integration. Moreover, this network was disrupted in dyslexics, confirming its essential role in audiovisual integration for reading. This study, for the first time, elucidates the neural basis underlying the development of audiovisual integration for reading.

Keywords: audiovisual integration; reading; development; brain network; fMRI

Introduction

Establishing reliable and robust associations between visual and auditory information forms the foundation of reading acquisition and development [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. Dysfunction in integrating orthographic and phonological information into a unified audiovisual percept has been identified as a critical factor in reading failure across both alphabetic [?, ?, ?] and logographic languages [?, ?, ?, ?, ?, ?]. Congruent phonological information and visual scripts complement each other, thereby improving the accuracy and speed of visual word recognition [?, ?, ?, ?, ?, ?, ?, ?].

At the neural level, numerous neuroimaging studies using different task paradigms have identified several brain regions involved in audiovisual integration for reading. For example, by comparing brain activation between audiovisual responses and the summation of unisensory responses, Raij et al. (2000) and van Atteveldt et al. (2004) found that the bilateral superior temporal gyrus/superior temporal sulcus (STG/STS), left frontoparietal region, and right frontal cortex were engaged in the integration of letters and speech sounds in skilled adult readers [?, ?, ?]. Additionally, several studies have examined the brain substrates of audiovisual integration using the congruency effect, which compares brain responses between congruent and incongruent audiovisual stimulus pairs [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. Studies of adult readers have found that the bilateral STG/STS, Heschl' s sulcus/planum temporale, middle/inferior temporal gyrus (MTG/ITG), middle/inferior frontal gyrus (MFG/IFG), cingulate gyrus (CG), superior parietal lobule (SPL), and fusiform gyrus (FuG) were engaged in audiovisual integration processing [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. In short, brain activation in the superior temporal cortex and frontal cortex has been consistently observed to support audiovisual integration in reading processing.

With practice and reading development, audiovisual integration processing becomes gradually automatic and optimal [?, ?, ?, ?, ?, ?]. A study of Dutch children showed that processing time for letter-speech sound associations steadily decreased over the full range of primary school grades, despite early acquisition of associations between orthography and phonology [?, ?], suggesting ongoing development toward automatic processing. Furthermore, Froyen et al. (2009) found that skilled adult readers, but not children (10–12 years), showed enhanced mismatch negativity (MMN) amplitude when letter-speech sounds were presented simultaneously versus separately [?, ?], indicating differences in neural activity of audiovisual integration in reading between children and adults. To our knowledge, only one early study examined differences in effective connectivity of audiovisual integration between children and adults [?, ?, ?, ?], but that study examined audiovisual integration in the context of speech comprehension. Consequently, the differences in brain activity of audiovisual integration for visual word recognition (reading) between children and adults remain unknown.

Recent evidence shows that audiovisual integration requires interplay between distributed regions [?, ?, ?, ?, ?, ?, ?, ?]. Specifically, audiovisual integration recruits high-level cognitive processes (e.g., attention and semantic processing), resulting in its late development [?, ?, ?, ?, ?, ?, ?, ?, ?, ?], and thus regions involved in higher-order processing might interact with regions involved in audiovisual integration. In this context, large-scale functional network analysis may be a more informative method to understand the brain organization underlying audiovisual integration in reading and its development from childhood to adulthood. Functional networks are typically modeled as graphs composed of nodes (the cortical regions contributing to a network) and edges (the connections between nodes) [?, ?, ?, ?, ?, ?]. Previous studies have successfully applied network analysis methods to unveil the neurodevelopment of functional networks for reading [?, ?] and for expressive language ability [?, ?, ?, ?, ?].

Using functional network analysis, the present study aimed to unveil changes in the neural mechanisms underlying audiovisual integration for reading between children and adults. First, we compared the brain networks of audiovisual integration between normally developing child readers (9–12 years old) and skilled adult readers (20–28 years old). Following previous studies [?, ?, ?], a lexical decision task was used to examine audiovisual integration in a real reading context. Participants were asked to decide whether visual symbols presented simultaneously with congruent or incongruent speech sounds were real Chinese characters. The congruency effect was adopted as the index of audiovisual integration [?, ?, ?]. Our hypothesis was that compared to children, skilled adult readers would show greater functional connectivity in a widespread network involving core regions of audiovisual integration (such as STG, MFG, and IFG) and higher-order association cortices (such as prefrontal and parietal cortices).

Afterwards, the identified functional networks that differed between the two age groups were examined in a sample of children with developmental dyslexia. The rationale was that if these functional networks are critical to audiovisual integration development for reading, we would expect to observe disruption of these functional networks in individuals with dyslexia.

Materials and Methods

Participants

Twenty-five normally developing children (9 females, mean age = 11.45 ± 0.83 years, abbreviated as CH), twenty-one adults (11 females, mean age = 23.85 ± 2.61 years, abbreviated as AD), and fourteen children with dyslexia (4 females, mean age = 10.99 ± 1.03 years, abbreviated as DD) participated in this study. All participants were native Mandarin Chinese speakers and were right-handed as assessed by the Handedness Inventory (Department of Neurology, Beijing Medical University Hospital). All participants had normal hearing, normal or corrected-to-normal vision, and no history of ophthalmological or neurological abnormalities.

The sample size for CH and AD was determined a priori using G*Power (Version 3.1, http://www.gpower.hhu.de/) [?, ?, ?, ?, ?], which indicated that 34 participants were required for a medium partial ^{2} of 0.06 (effect size f = 0.25) and a power of 0.8 with an alpha of 0.05 [?, ?, ?, ?, ?, ?]. To compensate for potential exclusion of participants (e.g., excessive head motion), we recruited more than 20 participants for each group.

The dyslexic participants were drawn from a published study [?, ?]. The screening criteria included: (1) having a reading score at least one and a half standard deviations below the average score of children in the same grade, as assessed by the Character Recognition Measures and Assessment Scale (CRM) [?, ?]; (2) having a normal non-verbal intelligence quotient (IQ) score (above 85) on the Combined Raven' s Progressive Matrices (CRT) [?, ?, ?, ?]; and (3) not meeting criteria for ADHD according to the Chinese Classification of Mental Disorder 3 (CCMD-3).

The study was approved by the ethics committee of the Institute of Psychology, Chinese Academy of Sciences. All adult participants and guardians of child participants provided written informed consent prior to participation. Demographic information and screening test results are shown in Table 1 .

Linguistic-Cognitive Tests

All participants completed three linguistic-cognitive tests measuring reading accuracy, reading fluency, and phonological awareness. The reading accuracy test consisted of 172 Chinese characters with varying word frequencies. Participants were required to overtly name all characters as accurately as possible with no time limit. The reading fluency test consisted of 160 high- and medium-frequency Chinese characters. Participants were asked to read these characters aloud as quickly and accurately as possible within one minute. In both tests, one point was awarded for each correctly read character. The phonological awareness test presented participants with three syllables, one of which differed from the others in consonant, vowel, or tone (10 items for each type). Participants were asked to select the syllable that differed from the others, with one point given for each correct judgment. Three CH, six AD, and two DD participants did not complete the reading tests, so their scores on the linguistic-cognitive tests were missing. Test scores for the remaining participants are presented in Table 1.

Stimuli and Task Design

The visual stimuli consisted of 30 high-frequency Chinese characters and 30 pseudocharacters. All real characters were compound characters composed of a phonetic radical and a semantic radical. The pseudocharacters were created by combining a phonetic and a semantic radical in their legal positions in Chinese orthography, but were unpronounceable and nonsensical. Visual complexity (stroke number and frequency of radicals) was matched between real characters and pseudocharacters (see Supplementary Materials Table S1). The auditory stimuli consisted of 120 pronunciations of Chinese characters recorded by a female native speaker.

Stimuli were assigned to five experimental conditions: (1) audiovisually congruent characters (AVcon), in which a real character and its sound were presented simultaneously; (2) audiovisually incongruent characters (AVincon), in which a real character and an incongruent sound were presented; (3) audiovisual pseudocharacters (AVpseudo), in which a pseudocharacter appeared with the sound of a real character; (4) visual real characters (Vreal); and (5) visual pseudocharacters (Vpseudo), in which characters or pseudocharacters were presented visually in isolation.

An event-related design was adopted for fMRI scanning. Each participant underwent two runs. Each run included 15 trials of AVcon, 15 trials of AVincon, 30 trials of AVpseudo, 15 trials of Vreal, 15 trials of Vpseudo, and 47 null trials, for a total of 137 trials presented in pseudo-random order. In each task trial, a fixation was first presented at the center of the screen for 500 ms, followed by stimulus presentation for 1200 ms and a blank screen for 800 ms. Visual stimuli were presented for 1200 ms, and auditory stimuli were presented simultaneously with visual stimuli (in bimodal conditions), lasting 185–509 ms. Each null trial consisted of 500 ms of fixation and 2000 ms of a blank screen. Following previous studies [**?**, **?**, **?**], participants were instructed to complete a lexical decision task, attending to visual stimuli and determining whether they were real Chinese characters by pressing buttons.

Image Acquisition

All participants were scanned using a 3T Siemens Prismafit MRI scanner at the Beijing MRI Center for Brain Research of the Chinese Academy of Sciences. Functional MRI time series data were obtained using a BOLD-sensitive T2*-weighted gradient-echo echo planar imaging (EPI) sequence (32 slices, slice thickness = 3 mm with a 0.6-mm gap, in-plane resolution = 3 mm × 3 mm, flip angle = 90°, repetition time = 2500 ms, echo time = 30 ms). High spatial resolution anatomical images were acquired using a T1-weighted magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence (slice thickness = 1 mm, in-plane resolution = 1.0 mm × 1.0 mm, flip angle = 8°, repetition time = 2600 ms, echo time = 3.02 ms).

fMRI Data Analysis and Statistics

Preprocessing Image preprocessing was conducted using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/, Wellcome Department of Cognitive Neurology, University College London, London). The fMRI time series data were first corrected for slice timing and head motion, then normalized into Montreal Neurological Institute (MNI) stereotactic space with cubic voxels at 2 mm × 2 mm × 2 mm spatial resolution. Finally, normalized functional images were smoothed with an isotropic Gaussian kernel with a 6-mm full-width at half-maximum. Seven CH and two DD participants were excluded from subsequent analyses due to excessive head motion during scanning (> 3 mm translation or > 3° rotation), resulting in a final sample of 18 CH, 21 AD, and 12 DD subjects.

Functional Network Analysis **Creation of Functional Connectivity Matrices.** A total of 264 functional regions of 10-mm diameter spheres were selected as nodes based on a validated parcellation template [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**].

Functional connectivity (FC) matrices were created using the CONN Functional Connectivity Toolbox [?, ?]. Specifically, BOLD time series corresponding to the AVcon and AVincon conditions were extracted and concatenated separately over trials. Nuisance BOLD signal fluctuations from cerebrospinal fluid and white matter were estimated and removed using the anatomical component correction (CompCor) strategy [?, ?, ?, ?, ?]. Head motion (6 motion parameters and 6 first-order temporal derivatives) and the main effect of task were also regressed out. Data were high-pass filtered at 0.008 Hz to preserve task-relevant high-frequency signals, which have been found to yield stronger and more reliable evidence of age effects [?, ?, ?, ?, ?, ?]. Pearson' s correlation coefficients between each pair of regional time series were computed and transformed into Fisher' s z scores. Following this procedure, undirected and weighted 264×264 FC matrices were constructed for the AVcon and AVincon conditions for each participant [?, ?].

Network-Based Statistics. The network-based statistic (NBS) approach was used to identify functional networks underlying differences in audiovisual integration for reading between CH and AD [?, ?, ?, ?, ?, ?, ?, ?, ?], which has been widely used in neurodevelopment research [?, ?, ?, ?]. In the present study, we first detected significant nonzero connections [false discovery rate (FDR) corrected $p < 0.05$] in FC matrices for each group and condition by performing one-sample t-tests in GRETNA (http://www.nitrc.org/projects/gretna/) [?, ?]. A binary matrix was then created by performing a union of significant nonzero connections from the AVcon and AVincon FC matrices. The FC matrices masked by this 'union' binary matrix were inputted into NBS to identify significant audiovisual integration networks in the CH and AD groups, respectively. The 'union' binary matrix was used as a mask to keep the same edges for statistical comparisons [?, ?, ?]. A less constrained primary threshold of $p < 0.05$ was applied to retain more functional connectivity information for edges underlying neural differences between CH and AD. Supra-threshold connections were defined based on this primary threshold and used to determine topological components. A component (i.e., a subnetwork) is a connected graph for which a path can be found between any two nodes. Nonparametric permutation tests (5000 permutations, family-wise error rate (FWER) corrected $p < 0.05$) were then performed to estimate the significance of each subnetwork based on their intensities (the sum of test statistic values across all connections). The corrected p-value for a subnetwork of a given size was calculated as the proportion of permutations for which the largest component was the same size or greater. Hubs of the identified functional network for audiovisual integration were defined as nodes whose strength was 1.5 SD (standard deviation) greater than the mean strength across all nodes in the network [?, ?]. Node strength is analogous to node degree in weighted networks and is defined as the sum of edge weights (i.e., Fisher' s z scores) attached to a node [?, ?, ?, ?, ?].

As a final step, a 2 (group: CH and AD) $\times$ 2 (audio-visual congruency: AVcon and AVincon) repeated measures analysis of covariance (ANCOVA) was conducted in NBS with FC matrices masked by a binary matrix created from the union of significant networks involved in audiovisual integration in each group obtained in the previous step. Since head motion effects may confound between-group differences in functional connectivity [?, ?, ?, ?], average frame-wise displacement (FD) estimated from the six head movement parameters [?, ?, ?, ?, ?, ?] was calculated and included as a covariate. Additionally, since previous studies reported gender differences in audiovisual integration processing [?, ?, ?, ?, ?, ?], gender was also included as a covariate to control for potential effects. A primary threshold of $p < 0.01$ was applied to the ANCOVA, and subnetworks with FWER-corrected $p < 0.05$ were retained (5000 permutations). Functional network visualization was performed using BrainNet Viewer [?, ?, ?, ?].

Brain-Behavior Correlation Analyses To examine the relationship between reading ability and functional networks that differed across groups, correlation analyses were conducted between functional networks (the congruency effect of connectivity strength) and reading performance (reading accuracy, reading fluency, and phonological awareness) in the CH and AD groups, respectively. Additionally, to clarify the role of functional networks during lexical decisions with congruent and incongruent stimuli, we performed correlation analyses between functional networks (the congruency effect of connectivity strength) and in-scanner behavioral responses (accuracy and reaction time). The significance level was set at $p < 0.05$ after FDR correction for multiple comparisons.

Validation Analysis To evaluate the robustness of observed functional networks underpinning differences in audiovisual integration between CH and AD, three validation procedures were performed: (1) using a more stringent primary threshold of $p < 0.005$; (2) using another estimation method—NBS extent (the total number of connections within a component); and (3) using an alternative 200 ROI atlas created by Craddock et al. [?, ?, ?, ?, ?, ?].

Functional Network Analysis in Children with Developmental Dyslexia Given that audiovisual integration deficits in dyslexia may be caused by anomalies in neural development, we examined whether functional networks that differed between CH and AD were disrupted in children with dyslexia. Specifically, for each functional network showing significant differences between CH and AD, a binary matrix was first generated from the functional network. Each element of the binary matrix was set to 1 if it corresponded to a nonzero element (i.e., an edge) in the functional network; otherwise it was set to 0. We then multiplied the corresponding elements of the binary matrix and the FC matrix of DD in the AVcon/AVincon condition created in CONN, obtaining a new FC matrix for the DD group that was masked by the binary matrix. The sum of all elements in the triangles above or below the diagonal of the resulting matrix was taken as the network connectivity strength of the DD group.

Finally, we performed a 2 (group: CH and AD) × 2 (audio-visual congruency:

AVcon and AVincon) ANCOVA on the connectivity strength of the functional network. In addition to gender, Raven IQ scores were entered as a covariate in the analysis, as there was a significant difference in Raven IQ scores between the CH and DD groups [$t(28) = 2.16$, $p = 0.04$]. The significance level was set at $p < 0.05$ after FDR correction for multiple comparisons.

Results

Behavioral Performances

In-scanner behavioral data for one CH and three AD participants were not recorded due to technical reasons. Additionally, data from another three AD participants were excluded because their response accuracy was too low (< 0.73) and they were identified as outliers by boxplot analysis [**?**, **?**, **?**, **?**] in both AVcon and AVincon conditions. Accordingly, behavioral performance results were based on the remaining data from 17 CH and 15 AD participants.

Average accuracy in the AVcon and AVincon conditions was 0.89 (SD = 0.11) and 0.76 (SD = 0.19) for CH, and 0.98 (SD = 0.03) and 0.95 (SD = 0.05) for AD, respectively. Wilcoxon signed-rank tests showed that accuracy in the AVcon condition was higher than in the AVincon condition for both CH ($p = 0.009$) and AD ($p = 0.029$). Mann-Whitney tests showed that AD accuracy was higher than CH accuracy in both AVcon ($p < 0.001$) and AVincon ($p < 0.001$) conditions.

Average reaction time in the AVcon and AVincon conditions was 744.03 ms (SD = 68.12 ms) and 799.61 ms (SD = 84.59 ms) for CH, and 616.66 ms (SD = 76.13 ms) and 662.50 ms (SD = 83.82 ms) for AD. A 2 (group: CH and AD) $\times$ 2 (audio-visual congruency: AVcon and AVincon) ANCOVA with gender as a covariate revealed a significant main effect of group [$F(1, 29) = 22.37$, $p < 0.001$, partial $^2 = 0.44$], with CH showing longer reaction times than AD. The main effect of audio-visual congruency was near-significant [$F(1, 29) = 3.75$, $p = 0.063$], but the interaction between group and audio-visual congruency was not significant [$F(1, 29) = 0.33$, $p = 0.570$].

NBS Analysis Results

NBS analysis revealed a large-scale functional network (173 nodes and 273 edges) for the congruency effect (AVcon > AVincon) in AD, mainly encompassing intra-regional connectivity within the prefrontal, occipital, and limbic cortices, as well as inter-regional connectivity between prefrontal and temporal cortices, between prefrontal and parietal cortices, and between temporal and occipital cortices. Hubs included the left STG, right MTG, left lingual gyrus (LG), left cuneus, right middle occipital gyrus (MOG), right supramarginal gyrus (SMG), right insula, right precuneus, right CG, and right parahippocampal gyrus (PHG) [Figure 1: see original paper]. Additionally, a functional network (188 nodes and

280 edges) for the incongruency effect (AVincon > AVcon) was detected in AD, mainly including intra-regional connectivity within prefrontal, occipital, parietal cortices and the motor strip, and inter-regional connectivity between prefrontal and parietal cortices and between parietal cortex and motor strip. Hubs were the bilateral STG, bilateral IPL, bilateral postcentral gyrus (PostCG), left precuneus, left precentral gyrus (PreCG), right medial frontal gyrus (MedialFG), left insula, and bilateral CG [Figure 1: see original paper].

However, the contrast of AVcon > AVincon failed to identify a significant functional network in CH. The incongruency effect (AVincon > AVcon) was detected in a functional network (222 nodes and 368 edges) in CH, primarily encompassing intra-regional connectivity within prefrontal, occipital, parietal cortices and motor strip, and inter-regional connectivity between prefrontal and limbic cortices. Hubs were the bilateral LG, bilateral cuneus, right FuG, left MOG, right superior/middle/inferior frontal gyrus (SFG/MFG/IFG), bilateral inferior parietal gyrus (IPL), left PreCG, bilateral lentiform nucleus (LN), and right insula [Figure 1: see original paper].

Critically, the 2 (group: CH and AD) × 2 (audio-visual congruency: AVcon and AVincon) repeated measures ANCOVA identified a significant interaction between group and audio-visual congruency in a functional network comprising 5 nodes and 3 edges, which could be segmented into two subnetworks. The first subnetwork encompassed the left STG, right MedialFG, and right SFG, forming a prefrontal-superior temporal functional network [interaction effect: $F(1, 32) = 21.65$, $p < 0.001$, partial $^2 = 0.40$]. The second subnetwork comprised the left thalamus and right lentiform nucleus [interaction effect: $F(1, 32) = 15.75$, $p < 0.001$, partial $^2 = 0.33$]. In both subnetworks, the AD group showed a significant congruency effect (AVcon > AVincon) [first subnetwork: $F(1, 32) = 22.17$, $p < 0.001$, partial $^2 = 0.41$; second subnetwork: $F(1, 32) = 5.73$, $p = 0.023$, partial $^2 = 0.15$], while CH showed an incongruency effect (AVcon < AVincon) [first subnetwork: $F(1, 32) = 5.10$, $p = 0.031$, partial $^2 = 0.14$; second subnetwork: $F(1, 32) = 12.60$, $p = 0.001$, partial $^2 = 0.28$] [Figure 2: see original paper].

Correlation analyses revealed that in CH, the congruency effect (calculated by connectivity strength of the prefrontal-superior temporal network) correlated with reading accuracy ($r = 0.57$, FDR-corrected $p = 0.06$) and phonological awareness ($r = 0.70$, FDR-corrected $p = 0.018$), but not with reading fluency ($r = 0.42$, FDR-corrected $p = 0.162$). No significant correlations were found in the AD group (reading accuracy: $r = -0.05$, FDR-corrected $p = 0.883$; reading fluency: $r = -0.20$, FDR-corrected $p = 0.646$; phonological awareness: $r = 0.56$, FDR-corrected $p = 0.116$) [Figure 2: see original paper]. A Spearman correlation analysis showed that in the AD group, the congruency effect (calculated by connectivity strength of the prefrontal-superior temporal network) was positively correlated with accuracy in the AVincon condition ($r = 0.55$, uncorrected $p = 0.032$), while in the CH group, the correlation showed a similar trend but was not significant ($r = 0.39$, uncorrected $p = 0.125$).

Validation Results

The prefrontal-superior temporal network was replicated using the previous NBS procedure with a more stringent primary threshold ($p < 0.005$) and an additional estimation method based on NBS extent with a primary threshold of $p < 0.01$. However, analysis with a $p < 0.005$ threshold revealed no connectivity between the right SFG and right MedialFG, and analysis based on NBS extent revealed no connectivity between the left thalamus and right lentiform nucleus (Figure S1A). Using an alternative Craddock atlas, NBS analysis revealed a significant interaction between group and audio-visual congruency in a functional network involving the left MFG, right frontal pole, bilateral planum temporale/STG, and left lateral occipital cortex [interaction effect: $F(1, 32) = 11.76$, $p = 0.002$, partial $^2 = 0.27$; AD showed a significant congruency effect: $F(1, 32) = 11.82$, $p = 0.002$, partial $^2 = 0.27$; CH showed a near-significant incongruency effect: $F(1, 32) = 2.88$, $p = 0.099$, partial $^2 = 0.08$] (Figure S1B). These validation results highlight the reproducibility of the identified prefrontal-superior temporal network underpinning differences in audiovisual integration between children and adults.

Results of Functional Network Analysis in Children with Dyslexia

Since only the prefrontal-superior temporal network was identified in validation analyses, we examined this brain network in the dyslexic group. ANCOVA revealed a marginally significant interaction between group and audiovisual congruency [$F(1, 26) = 3.06$, $p = 0.092$, partial $^2 = 0.11$], but no significant main effects of group [$F(1, 26) = 1.10$, $p = 0.305$] or audiovisual congruency [$F(1, 26) = 1.53$, $p = 0.227$]. Simple effects analysis showed a significant incongruency effect (AVincon > AVcon) in CH [$F(1, 26) = 5.58$, $p = 0.026$, partial $^2 = 0.18$], but not in DD [$F(1, 26) = 0.20$, $p = 0.661$] [Figure 3: see original paper].

Discussion

The present study aimed to explore differences in functional brain networks supporting audiovisual integration for reading between children and adults. We found that during the lexical decision task, adults showed greater connectivity than children in a prefrontal-superior temporal network (encompassing the right medial frontal gyrus, right superior frontal gyrus, and left superior temporal gyrus) and a thalamus-lentiform nucleus network (encompassing the left thalamus and right lentiform nucleus), suggesting these networks are associated with the development of audiovisual integration for reading. Moreover, the prefrontal-superior temporal network was disrupted in children with dyslexia, confirming its essential role in audiovisual integration for reading. Taken together, our findings reveal, for the first time, the brain mechanisms of audiovisual integration for reading in adults and children as part of multimodal information processing in higher cognition.

Functional Networks of Audiovisual Integration for Reading

Much research has identified areas associated with audiovisual integration, including STG, MTG, MFG, IFG, FuG, LG, cuneus, IPL, precuneus, insula, and CG [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. To our knowledge, the present study is the first to identify functional brain networks of audiovisual integration for reading in both child and adult readers. Consistent with our predictions, audiovisual integration recruited a large-scale functional network in adults, involving intra-regional connectivity within the occipital cortex and inter-regional connectivity between temporal and occipital cortices and between prefrontal and temporal cortices. The left posterior STG was identified as the main hub, aligning with previous findings showing its core role in audiovisual integration for both speech and non-speech stimuli [?, ?, ?, ?, ?, ?, ?, ?]. When presented with incongruent audiovisual stimuli during a lexical decision task, both children and adults showed enhanced intra-regional connectivity within prefrontal, occipital, and parietal regions, as well as the motor strip, consistent with evidence implicating frontoparietal and pre-supplementary motor areas in response inhibition [?, ?, ?, ?].

A previous neural framework for reading [?, ?] proposed that connectivity within the occipital cortex reflects bottom-up transmission of visual features to ventral occipitotemporal cortex (vOT, including FuG and LG), and connectivity between STG and vOT reflects top-down generation of predictions formed from prior experience. Moreover, top-down processing is modulated by higher-order regions (prefrontal cortex) associated with attention and task demands [?, ?, ?, ?, ?, ?, ?]. In the current lexical decision task, input of auditory speech sounds might strengthen interaction between top-down and bottom-up hierarchies, which in turn affects recognition of visual characters. However, we did not detect significant networks in the AVcon > AVincon contrast in normally developing children. Presumably, children may be less sensitive to the audiovisual congruency effect during reading, given their lower level of linguistic knowledge and experience.

Functional Networks Underlying Developmental Changes in Audiovisual Integration for Reading

Network analysis revealed that in a prefrontal-superior temporal network, adults showed stronger connectivity in the AVcon condition than in the AVincon condition (congruency effect), while children showed the reverse pattern. The congruency effect (calculated by connectivity strength of the network) was positively correlated with reading accuracy and phonological awareness in children, but not in adults. This suggests that this brain network is vital to reading skill, particularly in developing readers. Indeed, previous studies have highlighted the role of phonology in reading [?, ?, ?, ?, ?, ?], and reliance on phonological processing is greater in children than in adults [?, ?]. Two nodes identified in the network—the MedialFG and SFG—are located in the prefrontal cortex (PFC) [?, ?], which is part of the associative cortex of the frontal lobe [?, ?, ?]. The PFC receives a wide array of sensory inputs from multiple modalities [?, ?, ?, ?, ?, ?, ?, ?] and has been hypothesized to support executive functions such as attention, inhibitory control, and decision-making [?, ?]. Specifically, bilateral MedialFG is generally involved in conflict detection [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?] and attentional control [?, ?, ?, ?, ?, ?]. Moreover, the right SFG has been reported to subserve conflict resolution mechanisms through top-down control of attentional resources [?, ?, ?, ?].

In addition to MedialFG and SFG, another critical node in the network is the left anterior STG. This finding aligns with previous studies reporting engagement of the anterior superior temporal cortex in letter-speech sound integration [?, ?, ?]. Furthermore, the anterior STG has been identified as a semantic hub enabling activation of semantic representations irrespective of input modality, such as written words, auditory sounds, and pictures [?, ?, ?, ?, ?, ?]. During reading, semantic, phonological, and orthographic representations are automatically accessed even when semantic processing is not required [?, ?, ?, ?, ?, ?, ?, ?], particularly in Chinese, which has direct mappings between orthography and semantics [?, ?]. Thus, in our lexical decision task, both phonological and semantic representations are activated [?, ?, ?, ?, ?], but given that semantic skills undergo prolonged development throughout childhood and adolescence [?, ?, ?, ?, ?, ?, ?], adults might automatically activate semantic representations whereas children might tend to activate phonological representations, reflected in connectivity differences in the anterior STG between children and adults.

There is anatomical evidence of structural projections from STG to PFC in nonhuman primates [?, ?, ?] and humans [?, ?]. The uncinate fasciculus and arcuate fasciculus are two main fiber tracts linking STG with PFC, forming anatomical substrates for transmission of auditory or multisensory information [?, ?]. Functionally, connectivity between STG and PFC has been linked to attention shifting [?, ?, ?, ?, ?, ?] and behavioral responses to visual stimuli [?, ?]. Attention is a vital factor for the late development of audiovisual integration skill [?, ?, ?] and has been found to mediate audiovisual integration processing at multiple stages (including visual and auditory processing, spatiotemporal realignment, congruency matching, and semantic analysis) in both bottom-up and top-down fashion [?, ?, ?, ?, ?, ?, ?, ?, ?]. According to the framework of multifaceted interplay between multisensory integration and attention [?, ?], audiovisual integration tends to occur pre-attentively (i.e., bottom-up) when speech inputs are congruent with visual characters, which in turn enhances perceptual processing of the task-relevant modality. In contrast, when speech input conflicts with visual character input, top-down attentional mechanisms are required to inhibit task-irrelevant stimuli that act as attention-capturing distractors. Evidence for such top-down mechanisms comes from the positive correlation between the prefrontal-superior temporal network and accuracy in the AVincon condition. Consequently, compared with developing children, maturation of the prefrontal-superior temporal network may allow skilled adult readers to take greater advantage of congruent phonology and suppress incongruent interference more effectively for recognition of visually presented characters.

Additionally, differences in audiovisual integration between children and adults were found in a thalamus-lentiform nucleus network (connectivity between left thalamus and right lentiform nucleus). The thalamus is an interface through which nearly all sensory information must pass before reaching the cerebral cortex [?, ?]. The lentiform nucleus is part of the striatum that receives massive projections from thalamus [?, ?]. Previous studies have demonstrated that the fronto-striato-thalamic pathway is associated with inhibitory capacity, which develops from childhood to adulthood [?, ?, ?, ?, ?]. Therefore, the subcortical thalamus-lentiform nucleus network may support inhibition of interference caused by incongruent auditory speech sounds. However, this result was not replicated in validation procedures and therefore requires further verification.

Disruption of the Prefrontal-Superior Temporal Network in Developmental Dyslexia

To further confirm whether the prefrontal-superior temporal network is a key neural circuit for audiovisual integration specific to reading, we examined this network in a group of dyslexic children with impaired reading skills. In line with our expectations, we observed disruption of the prefrontal-superior temporal network in dyslexic children. This result accords with previous evidence of abnormalities in a functional network composed of STG/STS and medial prefrontal cortex in German dyslexics during an audiovisual speech integration task [?, ?]. Since the prefrontal-superior temporal network is involved in cross-modal attention shifts [?, ?, ?], its disruption potentially signals difficulties in shifting attention between modalities in children with dyslexia, a phenomenon known as "sluggish attentional shifting" [?, ?, ?]. As a result, children with dyslexia may focus their limited attention resources on task-related visual stimuli (characters) and be less affected (facilitated or inhibited) by auditory input. Overall, the lack of a congruency/incongruency effect in children with dyslexia reveals atypical development of the prefrontal-superior temporal network. These findings further elucidate the neural foundations of developmental dyslexia and have potential to inform assessment and intervention programs [?, ?, ?].

Limitations

Several limitations should be considered in light of the present findings. First, we employed a visual lexical decision task to examine the effect of simultaneously presenting speech sounds and visual characters in a realistic reading context [?, ?, ?, ?]. However, further research is required to test whether our findings apply in the context of auditory perception—that is, the extent to which presenting visual information affects auditory perception during audiovisual integration processing.

Second, our findings apply to the Chinese writing system, which is non-transparent and drastically different from alphabetic languages in both visual features of written scripts and orthography-to-phonology correspondences. As previous studies have shown that audiovisual integration depends on orthographic transparency [?, ?], further work is necessary to examine the generalizability of the present results to transparent/semi-transparent writing systems.

Third, although the effective sample size of the present study meets requirements for acceptable statistical power, future studies with larger samples are needed to obtain more reliable and repeatable results. Additionally, further studies might consider recruiting participants from a wider age range and using a longitudinal design to assess changes in networks of audiovisual integration for reading along the neurodevelopmental trajectory.

Conclusion

The present study revealed differences in a prefrontal-superior temporal network involved in audiovisual integration for reading between normally developing children and skilled adult readers. These findings presumably reflect the effect of attention modulation in audiovisual integration. Additionally, the identified network was disrupted in children with developmental dyslexia, highlighting its importance in reading. We argue that this study is the first to unveil the neural mechanisms of audiovisual integration for reading in children and adults, potentially reflecting neurodevelopmental changes due to reading skill development and advancing our understanding of neural correlates of multimodal sensory integration in humans.

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Competing Interests

The authors declare that they have no competing interests.

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