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The influence of visual deprivation on the development of the thalamocortical network: Evidence from congenitally blind children and adults

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ABSTRACT

The thalamus is heavily involved in relaying sensory signals to the cerebral cortex. A relevant issue is how the deprivation of congenital visual sensory information modulates the development of the thalamocortical network. The answer is unclear because previous studies on this topic did not investigate network development, structure-function combinations, and cognition-related behaviors in the same study. To overcome these limitations, we recruited 30 congenitally blind subjects (8 children, 22 adults) and 31 sighted subjects (10 children, 21 adults), and conducted multiple analyses [i.e., gray matter volume (GMV) analysis using the voxel-based morphometry (VBM) method, resting-state functional connectivity (FC), and brain-behavior correlation]. We found that congenital blindness elicited significant changes in the development of GMV in visual and somatosensory thalamic regions. Blindness also resulted in significant changes in the development of FC between somatosensory thalamic regions and visual cortical regions as well as advanced information processing regions. Moreover, the somatosensory thalamic regions and their FCs with visual cortical regions were reorganized to process high-level tactile language information in blind individuals. These findings provide a refined understanding of the neuroanatomical and functional plasticity of the thalamocortical network.

1. Introduction

The structure and function of the human brain can undergo plastic changes due to sensory loss, cognitive training or skill acquisition (Gudi-Mindermann et al., 2018; Matuszewski et al., 2021; Pascual-Leone et al., 2005; Wang et al., 2020). One of the crucial issues within this topic is how neuroplasticity occurs in blind individuals. Studies have found that the visual cortices of blind individuals are functionally reorganized, responding to auditory stimuli (Abboud and Cohen, 2019; Bedny et al., 2011) and tactile stimuli (Beisteiner et al., 2015; Lingnau et al., 2012; Merabet et al., 2004) and engaging in advanced cognitive functions (e.g., language, memory, executive control and mathematics) (Abboud and Cohen, 2019; Bedny, 2017; Bedny et al., 2015; Burton et al., 2012; Kanjlia et al., 2016; Kim et al., 2017; Striem-Amit and Amedi, 2014; Wang et al., 2015). These studies mainly focused on plasticity in the cerebral cortices, although several studies have also begun to explore changes in the thalamus in blind individuals.

The thalamus is a large mass of gray matter located in the dorsal part of the diencephalon and is an important structure with regard to sensory transmission in the human brain (Sherman and Guillery, 2001). The thalamus, as one of the main hubs in the brain network (Crossley et al., 2013), structurally and functionally connects to many cortical regions (e.g., occipital, temporal and frontal regions) to support various cognitive functions (Geier et al., 2020; Hwang et al., 2017; Kafkas et al., 2020;

Abbreviations: AAL, automated anatomical labeling atlas; CHN-PD, Chinese pediatric; CS, calcarine sulcus; CUN, cuneus; DARTEL, Diffeomorphic Anatomical Registration Through Exponentiated Lie; FC, functional connectivity; FDR, false discovery rate; FWHM, full width at half maximum; GMV, gray matter volume; GRF, gaussian random field; IE, inverse efficiency; ITG, inferior temporal gyrus; LG, lingual gyrus; LGN, lateral geniculate nucleus; MNI, Montreal Neurological Institute; ROI, region of interest; rs-fMRI, resting-state functional magnetic resonance imaging; TIV, total intracranial volume; VBM, voxel-based morphometry; VL, ventral lateral nucleus; VOTC, ventral occipital temporal cortex; VPL, ventral posterolateral nucleus.

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Saalmann et al., 2012; Zhou et al., 2016), forming the thalamocortical network (Behrens et al., 2003; Fan et al., 2016; Müller et al., 2019; Tanaka and Kirino, 2017; Tu et al., 2020). Studies have demonstrated that visual deprivation leads to structural and functional changes in the thalamus itself and the thalamocortical network. For example, blind individuals showed decreased gray matter volume (GMV) in the thalamus (Cecchetti et al., 2016; Ptito et al., 2008). Huang et al. (2020) found that blind subjects exhibited reduced dynamic amplitude of low-frequency fluctuation values in the left thalamus. Decreases in white matter volume and fractional anisotropy values in the optic radiation have also been observed in blind individuals (Bridge et al., 2009; Noppeney et al., 2005; Pan et al., 2007; Ptito et al., 2008; Shimony et al., 2006; Shu et al., 2009). Blind persons showed increased functional connectivity (FC) strength in thalamo-occipital connections (Bedny et al., 2011; Heine et al., 2015; Liu et al., 2007; Müller et al., 2019) but decreased FC strength between the thalamus and the right lingual gyrus, Broca's area and primary somatosensory area (Huang et al., 2020; Ioannides et al., 2013; Sabbah et al., 2016). The abovementioned studies on the thalamus have mainly focused on adult blindness. Other studies have also observed that children with congenital visual impairment present an atrophic thalamus and optic radiations (Bathelt et al., 2020; Li et al., 2013; Ricci et al., 2006; Uggetti et al., 1997).

Tactile experience, especially braille learning, is important for blind people. Braille learning can lead to massive brain reorganizations. The left ventral occipital temporal cortex (VOTC) exhibited enhanced activity and strengthened functional connectivity with somatosensory cortices in sighted people after a short period of learning to read braille (Siuda-Krzywicka et al., 2016). The FC between the VOTC and the postcentral gyrus was stronger in low-vision subjects who had braille learning experience than in those who had not learned braille (Zhou et al., 2020). The visual cortex of blind individuals is involved in tactile processing (Beisteiner et al., 2015; Reich et al., 2011; Sadato et al., 2002). There have also been a few studies reporting that the lateral geniculate nucleus (LGN) of the blind is reorganized to process tactile information (Müller et al., 2019). However, the relations between tactile processing and the reorganization of the thalamocortical network in people with congenital blindness are not clear.

In brief, previous studies have elegantly revealed some pivotal mechanisms underlying structural and functional reorganization in the thalamocortical network. However, more research on these network alterations is required for the following reasons. First, no research has explored the effects of visual deprivation on the development of the thalamocortical network by examining multiple age groups in the same study. Second, there is a lack of systemic surveys of both structural and functional reorganization in the thalamocortical network. Finally, it is also unknown which behaviors concerning tactile processing are associated with neuroanatomical and functional changes in the thalamocortical network in blind individuals.

The present study aims to overcome the above shortcomings and to reveal how visual deprivation from birth influences the development of the thalamocortical network. We recruited 30 congenitally blind subjects and a control sample of 31 sighted subjects. Each sample included both children and adults. Structural 3D images, resting-state functional magnetic resonance imaging (rs-fMRI) images, and behavioral performance data for multiple cognitive tasks were collected for each subject. To elucidate how visual deprivation influences the development of the thalamocortical network, we successively performed three analyses: 1) ***regional gray matter volume (GMV) analysis in the thalamus*** to identify the vision/age-relevant thalamic regions; 2) ***FC analysis between the thalamus and cerebral cortex*** to identify the vision/age-relevant FCs with the vision/age-relevant thalamic regions; and 3) ***nodal GMV analysis in the cerebral cortex*** to identify the other vision/age-relevant cortical regions that were end nodes of the vision/age-relevant FCs. In each analysis, we first compared the brain measures among the four subject groups, and then calculated the correlations between these brain measures and behavior.

2. Materials and methods

2.1. Participants

We recruited four types of subjects from Beijing, China: congenitally blind children (n = 8), congenitally blind adults (n = 22), sighted children (n = 10) and sighted adults (n = 21) (Table 1). Between the two groups of children, there was no significant quantitative difference in sex distribution [males/females: 6/2 vs. 7/3; $\chi^2_{(1)} = 0.06$, $P = 1$], handedness (Oldfield, 1971) [right/left handed: 7/1 vs. 10/0; $\chi^2_{(1)} = 1.32$, $P = 0.44$], age [10.38 ± 2.50 years old vs. 10.8 ± 1.69 years old; $t_{(16)} = -0.43$, $P = 0.67$], or formal education level [5.38 ± 2.39 years vs. 5.50 ± 1.90 years; $t_{(16)} = 1.24$, $P = 0.90$]. Similarly, there was no significant difference between the two adult groups in sex distribution [7/15 vs. 10/11; $\chi^2_{(1)} = 1.12$, $P = 0.36$], age [24.14 ± 5.31 vs. 22.81 ± 2.58; $t_{(41)} = 1.03$, $P = 0.31$] or handedness [20/0 vs. 21/0; $\chi^2_{(1)} = 0$, $P = 1$], although there was a difference in the formal education level [14.00 ± 2.27 vs. 16.38 ± 1.86; $t_{(41)} = 3.76$, $P < 0.001$]. All blind subjects were congenitally blinded and reported having minimal light perception at most. The faint light perception of the blind slightly affected the structural organization and functional specialization of the visual parts of the thalamus (see details in Supplementary materials). All blind subjects had learned braille [children: 4.94 ± 2.27 years of experience; adults: 13.95 ± 2.24 years of experience] and had no other neurological disorders. Every sighted subject had normal or corrected-to-normal vision and reported having no history of neurological diseases. The present study was approved by the institutional review board of the State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University. Written informed consent was obtained from all participants prior to the experiments.

2.2. Imaging data acquisition

MRI data were collected from all subjects on the same 3T Siemens Prisma scanner in the Imaging Center for Brain Research at Peking University. Each subject took part in a structural T1-weighted scan (lasting for 10.62 min) and a rs-fMRI scan (lasting for 8.22 min). T1-weighted images were acquired using a 3D magnetization-prepared rapid gradient echo sequence with the following parameters: 192 sagittal slices; slice thickness = 1 mm; gap = 0.5 mm; repetition time = 2530 ms; echo time = 2.98 ms; voxel size = 0.5 × 0.5 × 1.0 mm; flip angle = 7°; inversion time = 1100 ms; and field of view = 256 × 256 mm. The rs-fMRI data were obtained with an echo-planar imaging sequence while the participants kept their eyes closed. The parameters of this sequence were as follows: 64 axial slices, slice thickness = 2 mm; gap = 0.2 mm; repetition time = 2000 ms; echo time = 30 ms; voxel size = 2 × 2 × 2 mm; flip angle = 90°; and field of view = 224 × 224 mm.

2.3. Behavioral data collection

To identify the behaviors that were associated with thalamus-related neural regions or FCs, participants were asked to complete two behavioral tasks before or after scanning. The two tasks (i.e., verb generation and nonword reading) were used to evaluate advanced language abilities in the processing of real words and nonwords, respectively.

For the sighted individuals, all the stimuli were visually presented on the PC screen using the DMDX program (Forster and Forster, 2003). The stimuli were presented to the blind subjects in tactile form using the following three-step process. The stimuli were first presented on a PC screen, then translated into braille by a screen reader (NonVisual Desktop Access, https://www.nvaccess.org/), and finally presented on a braille display device (THDZ-40, https://www.qhqmx.com.cn). Each task was individually administered in a separate session. The presentation order of the items was pseudorandom and identical across subjects in all groups. The accuracy and reaction time of the subjects' responses to each item were recorded.

Table 1
Demographic characteristics of the participants.

Subject	Gender	Handedness	Years of age	Years of education	Cause of blindness	Light perception	Years of Braille learning
Blind children							
1	F	R	9	4	ONA	Faint	2.5
2	F	R	11	6	ONH	Faint	5
3	M	L	13	7	ONA	None	7
4	M	R	8	4	ROP	None	4
5	M	R	8	3	ROP	None	3
6	M	R	9	4	CM	None	3
7	M	R	10	6	ED	Faint	6
8	M	R	15	10	ED	Faint	9
Blind adults							
1	F	R	19	13	GRP	Faint	13
2	F	R	19	13	ONA	Faint	13
3	F	R	19	12	Unknown	Faint	12
4	F	R	19	13	Unknown	Faint	13
5	F	R	19	9	Unknown	Faint	9
6	F	R	20	14	ED	None	14
7	F	R	21	9	MH	Faint	9
8	F	R	22	15	ONA	None	15
9	F	R	22	15	Unknown	Faint	15
10	F	R	23	16	ROP	None	16
11	F	R	25	12	Cataracts	None	12
12	F	R	26	17	Unknown	None	17
13	F	R	27	15	ONA	None	15
14	F	R	29	12	ONA	Faint	12
15	F	R	35	15	Unknown	None	15
16	M	R	20	14	ROP; ONA	None	14
17	M	R	20	14	Unknown	Faint	14
18	M	R	25	16	Unknown	Faint	16
19	M	R	26	15	FD	Faint	15
20	M	R	26	18	Unknown	Faint	18
21	M	R	32	15	ED	None	15
22	M	R	37	16	Unknown	None	15
Sighted children							
1	F	R	9	4	/	/	/
2	F	R	10	4	/	/	/
3	F	R	11	6	/	/	/
4	M	R	9	4	/	/	/
5	M	R	9	3	/	/	/
6	M	R	11	5	/	/	/
7	M	R	11	6	/	/	/
8	M	R	11	6	/	/	/
9	M	R	13	8	/	/	/
10	M	R	14	9	/	/	/
Sighted adults							
1	F	R	18	12	/	/	/
2	F	R	20	14	/	/	/
3	F	R	20	14	/	/	/
4	F	R	20	14	/	/	/
5	F	R	21	15	/	/	/
6	F	R	21	15	/	/	/
7	F	R	21	17	/	/	/
8	F	R	24	17	/	/	/
9	F	R	24	17	/	/	/
10	F	R	26	18	/	/	/
11	F	R	27	19	/	/	/
12	M	R	22	16	/	/	/
13	M	R	22	16	/	/	/
14	M	R	23	16	/	/	/
15	M	R	23	17	/	/	/
16	M	R	23	17	/	/	/
17	M	R	23	17	/	/	/
18	M	R	23	17	/	/	/
19	M	R	23	18	/	/	/
20	M	R	27	19	/	/	/
21	M	R	28	19	/	/	/

Note. CM = congenital microphthalmos; ED = eyeball dysplasia; *F* = female; FD = fundus dysplasia; GRP = genetic retinitis pigmentosa; *L* = left; *M* = male; MH = macular hypoplasia; ONA= optic nerve atrophy; ONH= optic nerve hypoplasia; *R* = right; ROP = retinopathy of prematurity. The handedness was evaluated using Edinburgh Handedness Inventory (Oldfield, 1971).

Nonword reading. We assessed 40 nonwords in the adult group and 20 nonwords in the child group. Each nonword consisted of two Chinese characters (e.g., 起男*/qi3nan2/;* the word was written as "起男", whose pinyin is */qi3nan2/*) and had no meaning. The Chinese characters were high-frequency words and were familiar to both the blind and sighted groups. Participants were required to read the nonwords aloud.

Verb generation. For each item, a Chinese object noun (e.g., 改锥*/gai3zhui1/*screwdriver) was presented, and the subjects were required to speak one verb associated with the noun (e.g., 拧*/ning3/*twist). We used 60 items for the adult group and 20 items for the child group. The Chinese object nouns were high-frequency words and were familiar to both the blind and sighted groups.

For each item, the subjects were instructed to make responses as quickly and accurately as possible. The responses of the tasks were digitally recorded and transcribed. The two behavioral tasks included more items for adults than for children because the tasks were time consuming for children. The items for the children were randomly selected from those for adults and were identical across children. The accuracy and reaction time of each response were recorded. To correct for speed-accuracy trade-off effects, behavioral performance was expressed as an inverse efficiency (IE) measure—the average response time for the correct items divided by the accuracy (Townsend and Ashby, 1983). The negated IE (-IE) was used in our analyses such that higher values would reflect better performance.

2.4. Imaging data preprocessing

For each child, DPABI 4.3 (http://rfmri.org/; Yan et al., 2016) was applied to perform the preprocessing of rs-fMRI data. It mainly included the following steps. 1) The 5 initial volumes of each run were discarded; 2) Slice timing and head motion correction were performed. Participants whose head motion exceeded 3 mm of translation or 3° of rotation throughout the course of the scans were excluded, as were patients whose mean framewise displacement was more than 0.5 mm. Head motion did not differ between the groups (*Ps* > 0.05). 3) New segmentation and the Diffeomorphic Anatomical Registration Through Exponentiated Lie (DARTEL) algorithm (Ashburner, 2007) were used to coregister the functional images with the T1 images and then spatially normalize the images to the Chinese pediatric (CHN-PD) atlas (https://www.nitrc.org/projects/chn-pd/; Zhao et al., 2019). 4) The voxels were resampled to 1.5 × 1.5 × 1.5 mm; 5) The spatially normalized images were smoothed using a Gaussian kernel with a 4-mm full width at half maximum (FWHM). 6) A temporal bandpass filter (0.01–0.1 Hz) was applied to reduce the low-frequency drift and high-frequency noise. 7) To exclude physiological noise and the influence of head motion, the mean signals of the white matter, cerebrospinal fluid and Friston's 24 parameters were regressed out from the resting-state fMRI time series. Friston's parameters were derived from the Friston 24-parameter model of head movement (Friston et al., 1996), which incorporates 6 standard head motion parameters, 6 head motion parameters one time point before, and the 12 corresponding squared items (Power et al., 2014; Yan et al., 2013). These parameters have been widely used to correct head motion in resting-state fMRI scans (Sato et al., 2019; Sbaihat et al., 2021; Xia et al., 2022).

The DPARSF toolbox-based software Statistical Parametric Mapping 12 (SPM 12; http://www.fil.ion.ucl.ac.uk/spm) in DPABI 4.3 was used for VBM preprocessing and subsequent analyses. The specific process for each child's images was as follows. First, the scalps and skulls were removed from the T1 structural images. Second, using the DARTEL algorithm and applied tissue probability maps from the CHN-PD atlas, we segmented the T1 structural images into three tissue types: gray matter, white matter, and cerebrospinal fluid. At the same time, we obtained a group template that was registered to the pediatric space (i.e., the CHN-PD atlas) via affine transformation. Third, each subject's segmented structural images in the native space were coregistered into the pediatric space (i.e., CHN-PD atlas) by using the group template so that each subject's segmented structural images were spatially normalized. Fourth, the gray matter partitions of the structural images were modulated by the determinants of the Jacobians derived from the transformation parameters (Ashburner and Friston, 2001; Goldszal et al., 1998). Finally, the modulated, normalized GM images (representing GMV, voxel size 1.5 × 1.5 × 1.5 mm) were smoothed using a Gaussian kernel with a 4-mm FWHM, and the preprocessed GMV images of each group were obtained for subsequent analysis.

For each adult, the preprocessing steps were identical to those described above for the children, with the exception that the images were spatially normalized to Montreal Neurological Institute (MNI) space instead of the CHN-PD atlas.

To compare images between children and adults in the same space, we translated the children's preprocessed images in the pediatric space to the adult MNI space (Fan et al., 2021; Xia et al., 2022; Zhao et al., 2019). Specifically, we first performed spatial normalization between the T1 child template in the CHN-PD space (i.e., CHN-PD atlas) and the T1 adult template in the MNI space (i.e., MNI template) using the function *normalize (estimate)* in SPM12. This generated the normalization parameters. Then, the normalization parameters were used to transform the children's images in the pediatric space to the adult MNI space using the function *normalize (write)* in SPM12. Thus, we obtained pediatric images spatially normalized to the adult MNI space. To further examine whether the statistical results in the thalamus were different between two types of normalization approaches (i.e., whole-brain-based normalization and thalamus-based normalization), a control analysis was performed (see details in Supplementary materials).

2.5. Statistical analysis

2.5.1. Regional gmv analysis in the thalamus

Group difference in GMV of the thalamus. To identify the thalamic regions with significant differences based on development in the four groups of participants, we performed a two-way analysis of covariance (ANCOVA): 2 levels for vision (blind vs. sighted) * 2 levels for age (children vs. adults). The dependent variable was the GMV value of the subjects in each voxel of the thalamus. Total intracranial volume (TIV) and gender were the covariates of no interest (Barnes et al., 2010; Peelle et al., 2012; Pell et al., 2008). The TIV was calculated as the sum of the normalized, modulated tissue segments (gray matter, white matter, and cerebrospinal fluid). Note that all the two-way ANCOVAs and ANOVAs adopted these two independent variables (i.e., vision and age) unless otherwise noted. The clusters with significant main effects or interactions in the thalamus were extracted for post hoc comparisons. The thalamus was masked according to the automated anatomical labeling atlas (AAL; Rolls et al., 2015). This atlas divided the thalamus into 30 regions with a bilaterally symmetric distribution, i.e., 15 pairs of regions. Gaussian random field (GRF) correction (voxel-level $P < 0.001$, cluster-level $P < 0.05$) was utilized to correct for multiple comparisons after ANCOVA. The false discovery rate (*FDR*) correction ($q < 0.05$) was utilized to correct for multiple comparisons among post hoc *t*–tests.

Thalamic GMV-behavior correlation analysis. This analysis was performed to identify the cognitive behaviors that were associated with the thalamic regions identified in the above analysis. For simplicity, we considered only the thalamic regions with significant interactions with vision and age in the aforementioned analysis, and these regions were defined as the regions of interest (ROIs). We first extracted the mean GMV values (i.e., residual GMV values, from which we regressed out the influence of TIV and gender on basis of all the 61 subjects) in each ROI for each subject. Then, we conducted Spearman rank partial correlations between mean GMV values and performance in each of two behavioral tasks across subjects in each subject group. *FDR* correction ($q < 0.05$) was implemented to adjust for multiple comparisons. To avoid the influence of outliers, a blind child who performed poorly in all the behavioral tasks was excluded from this analysis.

2.5.2. FC analysis between the thalamus and cerebral cortex

Group difference in FC between the thalamus and cerebral cortex. To identify the FCs involving the thalamic regions that showed significant interactions of vision and age in the aforementioned analysis, we carried out the following analyses of the rs-fMRI data. For each subject, we first extracted the strength of the averaged blood oxygenation level–dependent (BOLD) signal at each time point for each voxel across the whole brain. Second, each of the ROIs identified in the above analyses was treated as a seed, and the signal strength value at each time point in all voxels within the seed was averaged. Third, the averaged signal strength in the seed was correlated with the signal strength of each voxel outside the seed across time points, and a correlation coefficient was obtained in relation to each voxel outside the seed. Fourth, the correlation coefficients in the whole brain, excluding the seed, were subjected to the Fisher *r*-to-*z* transform, and an FC map was obtained for each subject in which the *z* value of a voxel represented the FC strength between the voxel and the seed. Finally, analyses of subject group differences were performed for each seed, i.e., two-way ANOVA. The dependent variable was extracted as the *z* values of FC strength between the voxel and the seed associated with significant main effects or interactions in the thalamus (*GRF* corrected, voxel-level $P < 0.001$, cluster-level $P < 0.05$).

FC-behavior correlation analysis. To identify the cognition-related behaviors associated with the functional connections that had significant interactions with vision and age in the above analysis, we again performed a Spearman rank correlation between the mean strength of each functional connection with a significant interaction in the above analysis and performance in each of the two tasks across subjects. *FDR* correction ($q < 0.05$) was implemented to adjust for multiple comparisons. To eliminate the confounding influence of the two nodes joined by the FC, the averaged GMV value of each node was regressed out as well (Chabran et al., 2020; Dukart and Bertolino, 2014; Li et al., 2021; Newton et al., 2012; Shafiei et al., 2020; Wang et al., 2015).

2.5.3. Nodal GMV analysis in the cerebral cortex

Group difference in GMV of cortical nodes connected with thalamic FCs. The aforementioned analysis showed that the FC strength itself and one of the two nodes (i.e., the thalamic seed) in the FCs that had significant interactions in ANOVA were both significantly correlated with visual experience and age change. To further investigate the pattern of the GMV values of another node (i.e., the cortical endpoint/node) in the connection in the four groups, we performed two-tailed independent samples *t*-tests (*FDR* corrected, $q < 0.05$) to compare the mean GMV values (i.e., mean residual GMV values, in which TIV and gender were regressed out) between the four subject groups.

Cortical nodal GMV-behavior correlation analysis. We again carried out brain-behavior correlation analyses for the cortical nodes of FCs with significant interactions. We correlated the mean residual GMV value in each of the cortical nodes with performance in each of the two tasks across subjects (*FDR* corrected, $q < 0.05$).

3. Results

3.1. Behavioral performance of participants

Participants' mean accuracies and reaction times on the two behavioral tasks are shown in Table 2. For accuracy and reaction time in each task, we ran separate two-way ANOVA: 2 levels for vision (blind vs. sighted) * 2 levels for age (children vs. adults). The main effect of vision was significant for both accuracy and reaction time in all the tasks (*Ps* < 0.05). The sighted group performed more quickly and accurately in the tasks than the blind group. The main effect of age was not significant in the verb generation task for accuracy [$F_{(1, 57)} = 1.94$, $P = 0.17$] and reaction time [$F_{(1, 57)} = 0.12$, $P = 0.73$], while the effects were significant in the other task for either accuracy or reaction time (*Ps* < 0.05). The children performed worse than the adults. The interaction in the tasks did not reach the significance level (*Ps* > 0.05).

Table 2
Means (*SDs*) of accuracy (ACC) and reaction time (RT) in two tasks for four subject groups.

Subject	Measure	Nonword reading	Verb generation
Blind children			
	ACC	0.79 (0.19)	0.87 (0.19)
	RT (ms)	2563.88(1081.88)	4140.77 (1373.66)
Blind adults			
	ACC	0.93 (0.06)	0.89 (0.07)
	RT (ms)	2510.62 (668.35)	4344.53 (1362.00)
Sighted children			
	ACC	0.91 (0.06)	0.91 (0.10)
	RT (ms)	985.76 (208.88)	1799.87 (451.10)
Sighted adults			
	ACC	0.97 (0.03)	0.96 (0.03)
	RT (ms)	932.48 (205.02)	1790.12 (382.57)

3.2. Regional GMV analysis in the thalamus

Group difference in GMV of the thalamus. To identify the influence of congenital visual deprivation and brain development on thalamic structure, we conducted two-way ANCOVA based on regional GMV analysis in the thalamus. We extracted thalamic clusters with significant main effects and interactions (*GRF* corrected, voxel-level $P < 0.001$, cluster-level $P < 0.05$; see Fig. 1). Three clusters showed a significant interaction effect: the left lateral geniculate nucleus [lLGN; peak coordinates: $x = -25.5$, $y = -27$, $z = -4.5$; $F_{(1,57)} = 44.27$; 37 voxels], left ventral lateral nucleus/ventral posterolateral nucleus [lVL/VPL; peak coordinates: $x = -16.5$, $y = -15$, $z = 0$; $F_{(1,57)} = 59.03$; 221 voxels] and right VL/VPL [rVL/VPL; peak coordinates: $x = 16.5$, $y = -13.5$, $z = 0$; $F_{(1,57)} = 112.91$; 554 voxels] (Fig. 1A). To further reveal the pattern of the interaction in each significant cluster (i.e., ROI), independent samples *t*-tests (*FDR* corrected, $q < 0.05$) were performed to compare the mean GMV values (i.e., mean residual GMV values, in which the influences of TIV and gender were regressed out) between the four subject groups (Fig. 1B). These raw GMV values are presented in Supplementary materials. Regarding the two children groups, the GMV value in the lLGN was significantly lower in the blind children than in the sighted children [$t_{(17)} = 5.29$; $P < 0.001$], while the GMV values in the other two clusters (lVL/VPL and rVL/VPL) were significantly higher in the blind children than in the sighted children [$t_{(16)} > 4.23$; *Ps* < 0.001]. Regarding the two adult groups, the GMV value in the lLGN was marginally significantly higher in the blind adults than in the sighted adults [$t_{(41)} = 1.88$; $P = 0.07$]. There were no significant differences in GMV values in the bilateral VL/VPL between the two adult groups [lVL/VPL: $t_{(41)} = 1.53$; $P = 0.13$; rVL/VPL: $t_{(41)} = 1.72$; $P = 0.09$]. Regarding the two blind groups, the GMV value in the lLGN was significantly lower in the blind children than in the blind adults [$t_{(28)} = 3.07$; $P = 0.005$], while the GMV values in the other two clusters (lVL/VPL and rVL/VPL) were significantly higher in blind children than in blind adults [$t_{(28)} > 19.19$; *Ps* < 0.001]. Regarding the two sighted groups, the GMV values in all three clusters were significantly higher in the sighted children than in the sighted adults [$t_{(29)} > 3.9$; *Ps* < 0.001]. All *t*-test results reached the *FDR* corrected significance level ($q < 0.05$) except the results in the two adult groups. To better understand the anatomical and functional properties of the three thalamic clusters with significant interactions, we cross-referenced these regions with the Brainnetome Atlas (BNA; Fan et al., 2016). Based on this atlas, the lLGN is located in the occipital thalamus which transmits visual information (i.e., visual thalamus), and the bilateral VL/VPL lies in the sensory thalamus which transmits somatosensory information (i.e., somatosensory thalamus). The main effects of vision and age are reported in the Supplementary materials.

Thalamic GMV-behavior correlation analysis. For each subject group, we separately correlated the mean residual GMV values in each of the above three ROIs with significant interactions and performance

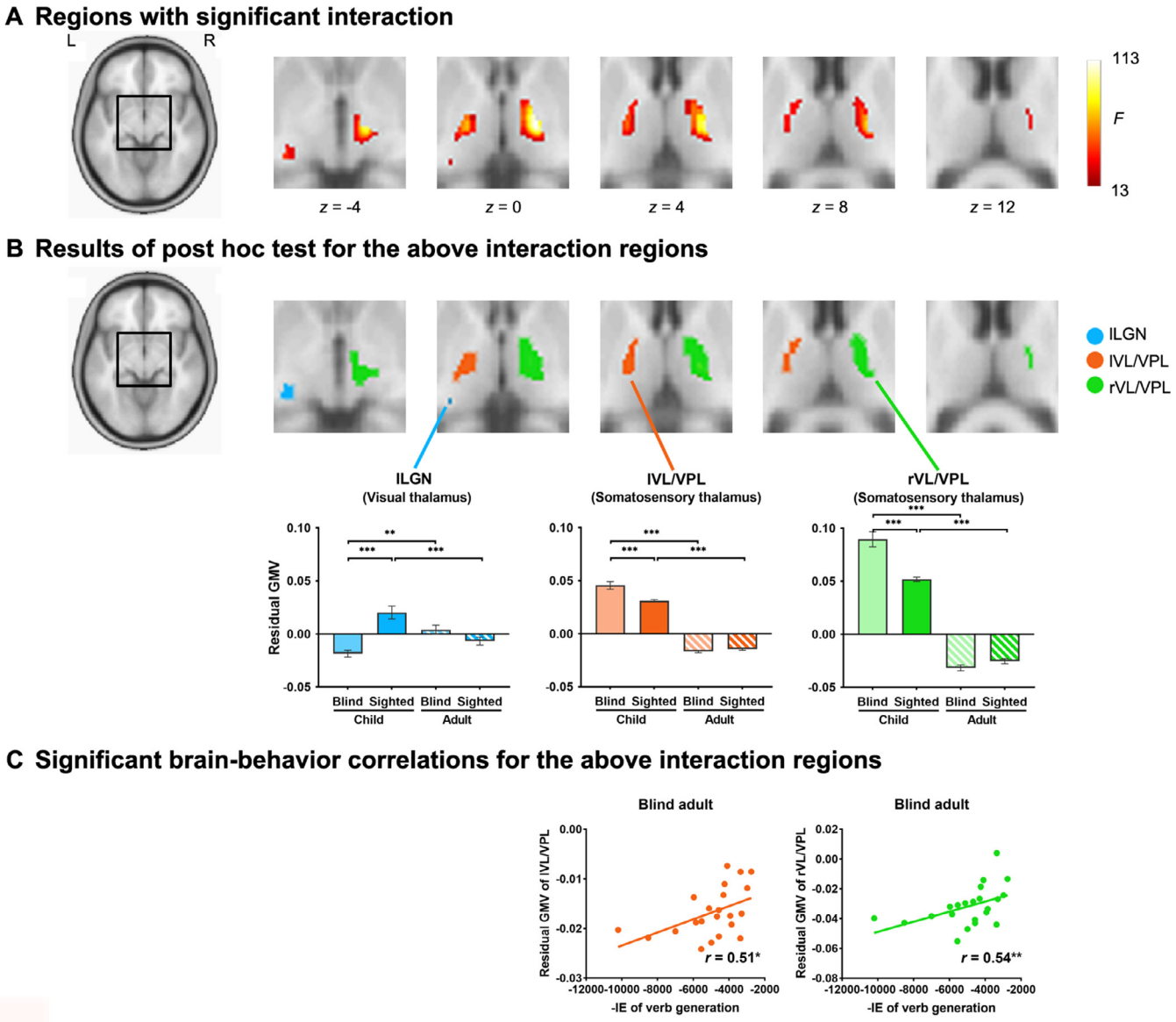

Fig. 1. Results of the regional GMV analysis within the thalamus. Two-way ANOVA: 2 levels for vision (blind vs. sighted) * 2 levels for age (children vs. adults). (**A**) illustrates the regions with a significant interaction effect in this analysis (Gaussian random field corrected, voxel-level $P < 0.001$, cluster-level $P < 0.05$). Error bars in (B) indicate the standard error of the mean (SEM). $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. GMV = gray matter volume; lLGN = left lateral geniculate nucleus; lVL/VPL = left ventral lateral nucleus/ventral posterolateral nucleus; rVL/VPL = right ventral lateral nucleus/ventral posterolateral nucleus; -IE = negated inverse efficiency.

in the two behavioral tasks across subjects (Table 3 and Fig. 1C). We observed that performance in the verb generation task was significantly positively correlated with the mean residual GMV values in bilateral VL/VPL regions in blind adults (lVL/VPL: $r = 0.51$, $P = 0.02$; rVL/VPL: $r = 0.54$, $P = 0.001$; *FDR* corrected, $q < 0.05$). The correlations in other groups were insignificant under *FDR* correction ($p > 0.05$).

3.3. FC analysis between the thalamus and cerebral cortex

Group difference in FC between the thalamus and cerebral cortex. For each thalamic ROI that showed a significant interaction in the above analysis, FC analysis was conducted to identify the vision/age-relevant functional connections from that ROI. In this analysis, we compared the connectivity strength values of each FC in the four subject groups using two-factor ANOVA (*GRF* corrected, voxel-level $P < 0.001$, cluster-level $P < 0.05$). The results of the interaction effect are shown in Fig. 2. A significant interaction effect was shown in four FCs: lVL/VPL-right lingual gyrus [rLG, peak coordinates: $x = 24$, $y = -87$, $z = -12$; $F_{(1,57)} = 20.80$; 14 voxels], lVL/VPL-right inferior temporal gyrus [rITG, peak coordinates: $x = 45$, $y = -72$, $z = -6$; $F_{(1,57)} = 22.91$; 14 voxels], lVL/VPL-right calcarine sulcus [rCS, peak coordinates: $x = 21$, $y = -69$, $z = 9$; $F_{(1,57)} = 20.57$; 61 voxels] and rVL/VPL-left cuneus [lCUN, peak coordinates: $x = 0$, $y = -87$, $z = 15$; $F_{(1,57)} = 24.65$; 60 voxels]. Regarding the two groups of children, the FC strength of all the connections was significantly lower in the blind children than in the sighted children [$t_{(16)} > 2.41$; $Ps < 0.03$]. Regarding the two groups of adults, the FC strength of all the connections was higher in the blind adults than in the sighted adults [$t_{(41)} > 4.46$; $Ps < 0.001$]. Regarding the two blind groups, the FC strength of all the connections was significantly lower in the blind children than in the blind adults [$t_{(28)} > 4.56$; $Ps < 0.001$]. There was no significant difference in the FC strength of any connection between the two sighted groups ($Ps > 0.05$), with the exception that the FC strength between the rVL/VPL and the rCS was significantly higher in the sighted children than in the sighted adults [$t_{(29)} = 2.15$; $P = 0.04$; see Fig. 3].

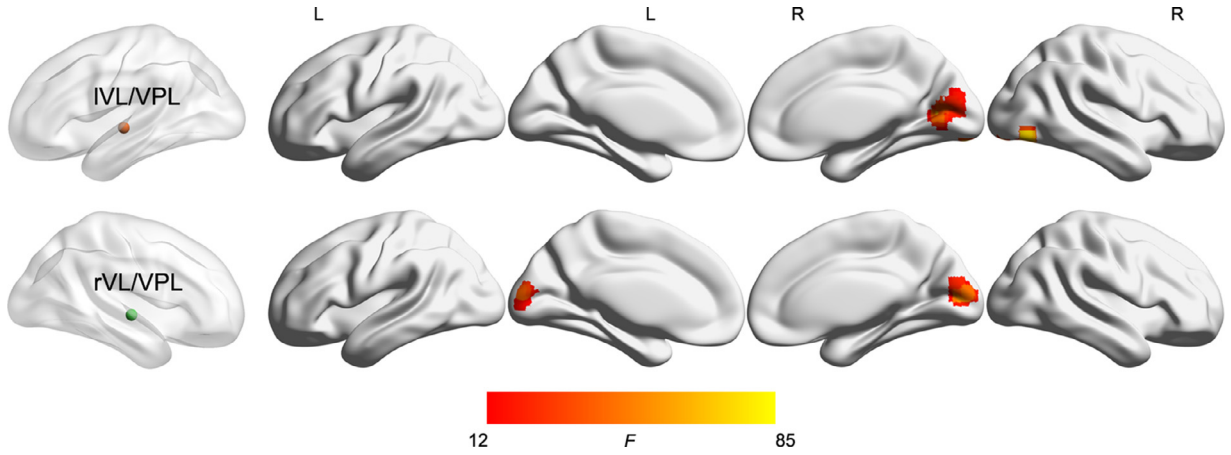

Fig. 2. Thalamocortical functional connections with significant interaction effects between the thalamus and the cerebral cortex. The seeds in the leftmost column functionally connect the regions in the other columns (Gaussian random field corrected, voxel-level $P < 0.001$, cluster-level $P < 0.05$). FC = functional connectivity; lCUN = left cuneus; lVL/VPL = left ventral lateral nucleus/ventral posterolateral nucleus; rCS = right calcarine sulcus; rLG = right lingual gyrus; rITG = right inferior temporal gyrus; rVL/VPL = right ventral lateral nucleus/ventral posterolateral nucleus.

Table 3
Correlation coefficients between the mean GMV values of three thalamic ROIs and performance in two tasks for four subject groups.

Subject	Task	lLGN	lVL/VPL	rVL/VPL
Blind children				
	Nonword reading	0.75	−0.07	−0.07
	Verb generation	0.36	0.11	0.11
Blind adults				
	Nonword reading	0.29	0.25	0.19
	Verb generation	0.40	0.51*	0.54**
Sighted children				
	Nonword reading	−0.42	−0.65*	−0.44
	Verb generation	−0.20	−0.44	−0.09
Sighted adults				
	Nonword reading	−0.04	0.07	0.07
	Verb generation	−0.06	−0.36	−0.18

Note. Spearman rank correlation was adopted.
* $P < 0.05$;.
** $P < 0.01$;*l* = left; LGN = lateral geniculate nucleus; *r* = right; VL = ventral lateral nucleus; VPL = ventral posterolateral nucleus.

All *t*-test results reached the *FDR* corrected significance level ($q < 0.05$) except the results in the two adult groups. The main effects of vision and age are reported in the Supplementary materials.

FC-behavior correlation analysis. For the four functional connections showing significant interactions in the above analysis, we correlated the mean FC strength value for each connection with the performance of the two tasks in each subject group (Table 4; Fig. 3). In the blind children group, the mean FC values for the rVL/VPL-lCUN connection were significantly positively correlated with performance in the nonword reading task ($r = 0.89$, $P = 0.01$, *FDR* corrected, $q < 0.05$). Regarding sighted groups, the mean FC values for the lVL/VPL-rCS connection in sighted children were significantly negatively correlated with performance in the verb generation task ($r = -0.84$, $P = 0.005$, *FDR* corrected, $q < 0.05$), and those for the rVL/VPL-lCUN connection in sighted adults were significantly positively correlated with performance in the verb generation task ($r = 0.58$, $P = 0.007$, *FDR* corrected, $q < 0.05$)

3.4. Nodal GMV analysis in the cerebral cortex

Group difference in GMV of cortical nodes connected with thalamic FCs. For the four nodes in the cortices (i.e., cortical nodes) that were part of the functional connections showing significant interactions in the above analysis, To reveal the pattern of nodal GMV values in the four groups, two-tailed independent samples *t*-tests (*FDR* corrected, $q < 0.05$) were performed to compare the mean GMV values (i.e., mean residual GMV values, in which TIV and gender were regressed out) between the four subject groups (Fig. 3). Regarding the two children groups, the GMV values in the lCUN [$t_{(16)} = 2.23$; $P = 0.04$; uncorrected] and rCS [$t_{(16)} = 2.13$; $P = 0.05$, *FDR* corrected $q < 0.05$] were significantly lower in the blind children than in the sighted children, while the GMV values in the other two clusters (rITG and rLG) were not significantly different between the two children groups (*Ps* > 0.05). There were no significant differences in GMV values between the two adult groups (*Ps* > 0.30), with the exception that the GMV values in the rITG in blind adults were lower than those in sighted adults [$t_{(41)} = 2.08$; $P = 0.04$, *FDR* corrected, $q < 0.05$]. Regarding the two blind groups, there were no significant differences in GMV values between the two blind groups (*Ps* > 0.05), with the exception that the GMV values in the rITG in blind adults were lower than those in blind children [$t_{(28)} = 2.82$; $P = 0.01$, *FDR* corrected, $q < 0.05$]. Regarding the two sighted groups, the GMV value in the lCUN [$t_{(29)} = 2.84$; $P = 0.01$; *FDR* corrected, $q < 0.05$] and rCS [$t_{(29)} = 5.22$; $P < 0.001$, *FDR* corrected, $q < 0.05$] was significantly lower in the sighted adults than in the sighted children, while the GMV values in the other two clusters (rITG and rLG) were not significantly different between the two sighted groups (*Ps* > 0.05)

Cortical nodal GMV-behavior correlation analysis. For the four nodes outside the thalamus that had significant FC with thalamic regions, no GMV-behavior correlations reached the *FDR*-corrected significance level ($q < 0.05$, Table 5).

4. Discussion

The structure and function of the brain remains plastic throughout life. The plasticity results from congenital and environmental causes, such as genetic genes, sensory-modality dominance, language-learning experience, developmental trajectory, and neural injury(Bavelier et al., 2006; Debanne et al., 2019; Draganski et al., 2004; Kral and Sharma, 2012; Lein et al., 2007; Lu et al., 2004). The blindness provides a window to explore the structural and functional plasticity of brain. Although previous studies have found the plasticity in the cerebral cortices in the blinds, what the structural and functional reorganizations occur in the thalamocortical network on a developmental scale after congenital visual deprivation is not clear. To explore how congenital visual deprivation influences the development of the thalamocortical network, we conducted GMV analysis, FC analysis, and brain-behavior correlation analysis in congenitally blind children and adults as well as sighted controls. We observed that blind subjects presented some reor-

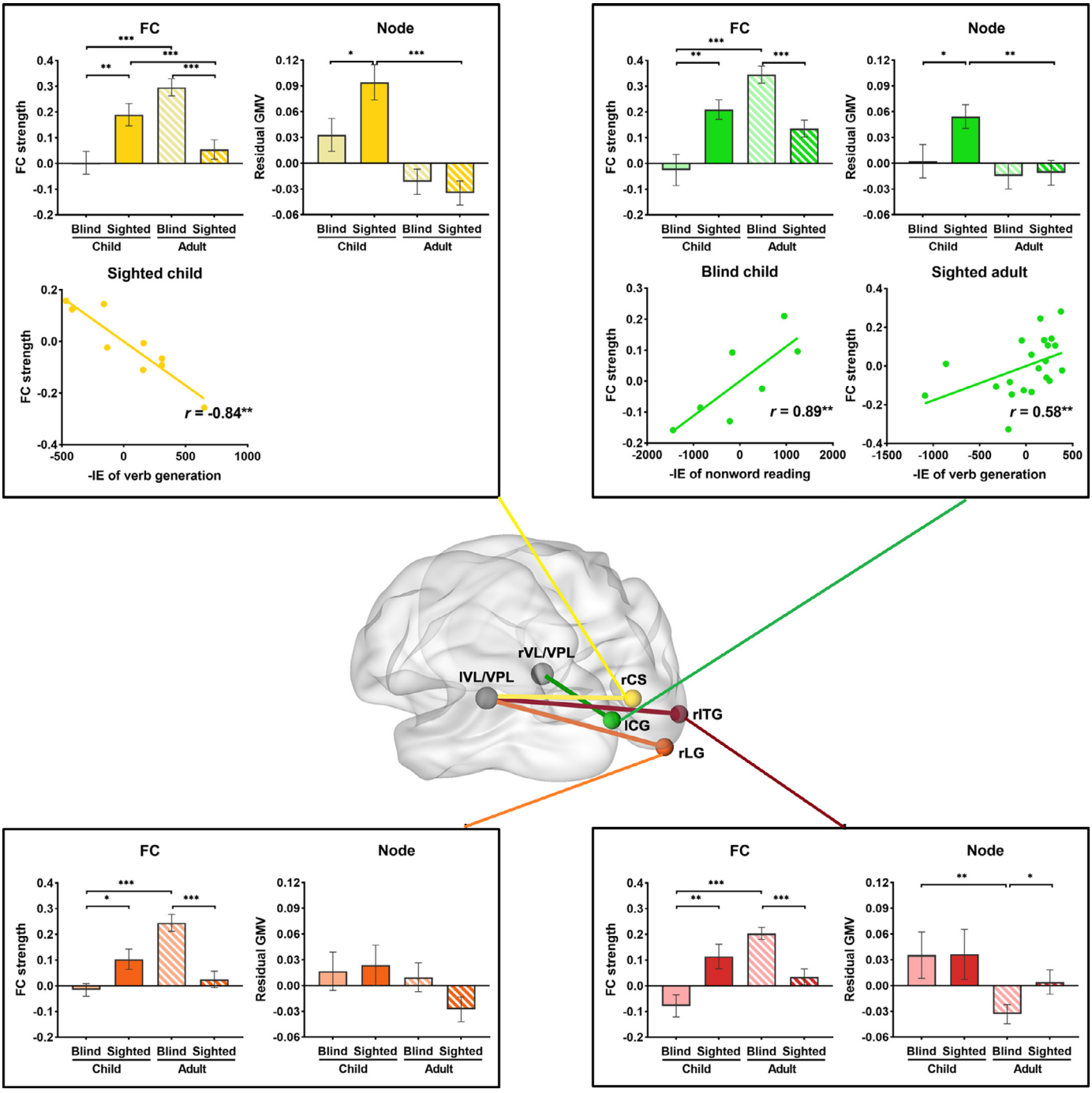

Fig. 3. Post hoc tests and brain-behavior correlations for the thalamocortical functional connections and their cortical nodes. The gray regions in the brain map are the thalamic seeds, and the other colored regions are the cortical nodes connected with the seeds. In each rectangle outside the brain map, the first row shows the post hoc test for the functional connection and its cortical node. Error bars indicate the standard error of the mean (SEM). The second row shows the significant brain-behavior correlations. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. FC = functional connectivity; lCUN = left cuneus; lVL/VPL = left ventral lateral nucleus/ventral posterolateral nucleus; rCS = right calcarine sulcus; rLG = right lingual gyrus; rITG = right inferior temporal gyrus; rVL/VPL = right ventral lateral nucleus/ventral posterolateral nucleus.

ganizations in structural gray matter, FC, and cognitive functions within the thalamocortical network relative to sighted subjects, reflecting the brain plasticity.

4.1. Structural reorganization of the thalamus in blind individuals

The results of regional GMV analysis in the thalamus provided direct evidence for anatomical thalamic rewiring in blind humans. We found that blind children had markedly lower GMV values in the "visual" thalamic regions than sighted children. The results suggest that an effect of visual deprivation on thalamic structure had already emerged at this early stage, in line with the observation of cerebral plasticity in blind children (Bedny et al., 2015). These changes in "visual" thalamic regions may be due to neuronal degeneration (Boucard et al., 2009). The "visual" thalamic neurons of blind children may have smaller, more globoid cytoplasm and smaller nuclei because of the lack of visual stimulation (Gupta et al., 2006). This is consistent with findings from animal research in visual thalamus reorganization after visual deprivation

Table 4
Correlation coefficients between the mean FC values of four FCs and performance in two tasks for four subject groups.

Subject	Task	lVL/VPL-lCUN	rVL/VPL-rCS	rVL/VPL-rLG	rVL/VPL-rITG
Blind children					
	Nonword reading	0.89**	0.11	0.29	−0.39
	Verb generation	0.64	−0.36	−0.46	−0.36
Blind adults					
	Nonword reading	−0.40	0.13	0.13	0.11
	Verb generation	−0.21	−0.16	−0.18	0.04
Sighted children					
	Nonword reading	0.25	−0.58	0.27	−0.24
	Verb generation	0.13	−0.84**	0.02	−0.48
Sighted adults					
	Nonword reading	−0.24	−0.02	0.03	0.09
	Verb generation	0.58**	0.20	0.33	0.06

Note. Spearman rank correlation was adopted.
*$P < 0.05$;
**$P < 0.01$;
CUN = cuneus; CS = calcarine sulcus; ITG = inferior temporal gyrus; *l* = left; LG = lingual gyrus; *r* = right; VL = ventral lateral nucleus; VPL = ventral posterolateral nucleus.
** $P < 0.01$;CUN = cuneus; CS = calcarine sulcus; ITG = inferior temporal gyrus; *l* = left; LG = lingual gyrus; *r* = right; VL = ventral lateral nucleus; VPL = ventral posterolateral nucleus.

Table 5
Correlation coefficients between the mean GMV values of five nodes outside the thalamus and performance in three tasks for four subject groups.

Subject	Task	lCUN	lLG	rCS	rITG
Blind children					
	Nonword reading	−0.07	0.11	−0.54	0.07
	Verb generation	−0.39	−0.32	−0.14	−0.54
Blind adults					
	Nonword reading	0.02	0.08	0.20	0.31
	Verb generation	0.28	0.07	0.41	0.25
Sighted children					
	Nonword reading	−0.52	−0.16	−0.33	−0.54
	Verb generation	−0.26	0.27	−0.10	−0.16
Sighted adults					
	Nonword reading	−0.12	0.02	−0.17	0.24
	Verb generation	0.28	0.29	0.02	0.48

Note. Spearman rank correlation was adopted.
CUN = cuneus; CS = calcarine sulcus; ITG = inferior temporal gyrus; *l* = left; LG = lingual gyrus; *r* = right.

(Ptito et al., 1996) and similar to prior studies on the visual cortex of blind individuals (Prins et al., 2016; Ptito et al., 2008). In contrast, we found that the blind children showed a hypertrophic somatosensory thalamus. This is consistent with predictions based on previous studies (Noppeney et al., 2005; Yu et al., 2007). These results may be interpreted in the context of neuronal development. Since our blind children had long-term experience of learning braille, the large amount of tactile stimulation might have promoted the development of somatosensory neurons. Literature has demonstrated that sensory and motor training induces changes in gray matter and white matter (Lövdén et al., 2010; Zatorre et al., 2012). For example, increased gray matter in the visual and somatosensory cortices has been reported after braille training (Bola et al., 2017; Matuszewski et al., 2021). As the somatosensory thalamus is an important part of sensory processing, the hypertrophic somatosensory thalamus of blind children in this study might be due to braille learning.

Interestingly, the pattern of GMV values in the "visual" thalamus changed in adulthood. Specifically, the GMV values in the lLGN from childhood to adulthood significantly increased in the blind group and significantly decreased in the sighted group. The GMV values in the lLGN were higher in the blind adults than in the sighted adults. The difference in the development pattern and the high GMVs in the visual thalamus of blind adults may be because a large amount of tactile input influenced the development of thalamic "visual" cells in the blind. One possible mechanism comes from the changes in the intrinsic connectivity between somatosensory and visual thalamic nuclei (Cecchetti et al., 2016). That is, when the somatosensory thalamus receives a large amount of tactile input, it may actively connect with the nearby visual thalamic regions and transfer the somatosensory information to them. Therefore, the visual thalamus actively developed and matured. These alterations might compensate for the GMV reduction because of visual deprivation in childhood and lead to the structural and functional reorganization of the "visual" thalamus (Chabot et al., 2007; Heil et al., 1991). In other words, the "visual" thalamus in blind subjects may engage in the processing of tactile information, which would prevent further atrophy of the "visual" regions.

Regarding the somatosensory thalamus, a changed pattern of GMV values was observed in the two adult groups relative to the two children groups. The GMV values in the somatosensory thalamus were not significantly different between the two adult groups while they were significantly different between the two children groups. Similarly, the hypertrophic somatosensory thalamus in blind children in this study might be due to braille learning (Bola et al., 2017; Matuszewski et al., 2021). Although the blind adults received more tactile input than the sighted adults, the GMVs in the somatosensory thalamus were not significantly different in the two adult groups. This may result from the interaction of multiple mechanisms, such as neuronal development and neuronal degeneration. We found that the development patterns between the blind and sighted groups were similar, in which the GMV values significantly decreased from childhood to adulthood. The development pattern was consistent with previous longitudinal thalamic studies, reporting that thalamic volume declined with age (Hughes et al., 2012; Sullivan et al., 2004). The underlying neurobiology of the reduced volume may be due to the degeneration of neuronal structures, including neuronal shrinkage, reductions in synaptic spines and reduced numbers of synapses (Terry et al., 1987).

Note that the mean GMV values of the visual thalamus in blind adults were marginally significantly higher than those in sighted adults in our study. The VBM results of our studies did not replicate the volumetric analysis of LGNs in congenital blindness, for example, finding a reduction in LGN volume in congenital blindness (Aguirre et al., 2016; Cecchetti et al., 2016). On the one hand, this might be due to the difference in methods of volume estimation between our analysis and previous volumetric analyses. The volume values were estimated through DPABI (http://rfmri.org/) (Yan et al., 2016) and SPM12 (http://www.fil.ion.ucl.ac.uk/spm) in the present study and through Tensor Based Morphometry or FSL (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL; Jenkinson et al., 2012;

Smith et al., 2004) in the literature (Aguirre et al., 2016; Cecchetti et al., 2016). On the other hand, this might be because of the difference in the braille learning experience of participants. The blind participants in our study had long-term experience with braille, whereas the duration of braille experience was not reported in prior volumetric analysis studies. The long-term learning of braille might promote the development and rewiring of the thalamus (Matuszewski et al., 2021; Müller et al., 2019; Zhou et al., 2020), which can compensate for the GMV reduction induced by degeneration and promote neuronal development. Further research is needed.

4.2. Reorganization of the thalamic functional network in blind individuals

The results of FC analysis showed that visual deprivation had a profound influence on the development of functional connections between the somatosensory thalamus and cortical "visual" regions as well as advanced information processing regions. In childhood, blind children showed weaker FC in those connections than sighted children. Regarding the FCs between the somatosensory thalamus and cortical visual regions, these changes in blind children might have been due to the absence of visual input, resulting in the degeneration of cortical visual neurons and weakened functions (Boucard et al., 2009; Prins et al., 2016). Moreover, the nodal GMV analysis in our study provided evidence that the GMV values of the lCUN and rCS in blind children were lower than those in sighted children. Indeed, the implicit mechanism is that FC, which reflects the synchronized neural activity of two brain regions (Li et al., 2015; Pais-Roldán et al., 2021), is based on the structure and structural connections of its related brain regions (Damoiseaux and Greicius, 2009; Shen et al., 2015). The structural development of the brain regions might influence the pattern of their neural activity. In other words, the reduced GMV due to injury or input deprivation might weaken the FCs of the relevant regions. Similarly, the rapid structural development of one brain region might induce active neural activity. When the neural activity of the two brain regions are equally active, the strength of this FC between them is strong. However, when the activity becomes differentially active (e.g., one region has stronger activation than another region), the strength of this FC becomes weak, reflecting the low synchronized neural activity of the two brain regions. We suggest that the changes in the FC strengh between the lVL/VPL and rITG in blind children might be related to the gray matter changes of the somatosensory thalamus (i.e., lVL/VPL). We found that the FC strengh between the lVL/VPL and rITG was lower in blind children than in sighted children. In addition, our regional GMV analysis in the thalamus revealed that the GMV values of the lVL/VPL were higher in blind children than in sighted children (Fig. 1B). This finding might be relevant to blind individuals learning braille during childhood (Cohen, 1966; Bola et al., 2017; Matuszewski et al., 2021). The large amount of input required to learn braille information might give rise to more rapid development of the somatosensory thalamus (i.e., lVL/VPL) and more active neural activity in the somatosensory thalamus of blind children. However, the GMV values of the rITG were comparable between blind and sighted children (Fig. 3). Hence, the weaker FC of blind children relative that of sighted children might be related to the overactivation of the lVL/VPL in the blind children. In the other words, overactivation led to be greater asynchrony between the somatosensory thalamus (i.e., lVL/VPL) and rITG in blind children than sighted children. The significant increase in the GMV values the of lVL/VPL in blind children might cause unsynchronized neural activity of two brain regions, inducing the weaker FC between these regions in blind children than in sighted children.

Nevertheless, the strength of these FCs from childhood to adulthood significantly increased in the blind, while that of most of them did not significantly change in the sighted. The strength of those FCs was stronger in blind adults than in sighted adults. These results indicate that the thalamic functional network in blind individuals integrated the visual cortical regions and high-level processing regions to support tactile information processing. Our findings were aligned with studies of reorganization in visual cortical regions deprived of visual stimulation; such studies reported the involvement of visual cortical regions in tactile processing (Abboud and Cohen, 2019; Amedi et al., 2004; Burton et al., 2012; Jiang et al., 2015; Ptito et al., 1996). This may have been related to long-term braille learning and brain development (Bola et al., 2017; Siuda-Krzywicka et al., 2016; Zhou et al., 2020). Previous studies showed that the activation in the visual cortex and the functional connectivity between the visual and somatosensory/motor cortices in sighted subjects became stronger after braille training (Bola et al., 2017; Siuda-Krzywicka et al., 2016), demonstrating that tactile training induced functional plasticity in the visual cortex.

The increases in FC in the blind group may have multiple intrinsic mechanisms. One is the unmasking hypothesis (Cohen Kadosh and Walsh, 2006; Hamilton and Pascual-Leone, 1998; Rauschecker, 1995; Wittenberg et al., 2004), proposing that visual deprivation can unmask and strengthen the preexisting structural or functional connections due to the cognitive pluripotency of brain regions (Bedny, 2017), in conjunction with environmental demands. For example, previous FC studies found that tactile stimulation enhanced activity in the visual cortex that supported visual processing in sighted subjects (Macaluso et al., 2000). This finding indicates that the FCs between the somatosensory thalamus and visual cortical regions may preexist and that repeated somatosensory input may unmask and strengthen them. Moreover, brain structural studies found that visual deprivation led to changes in the thalamo-occipital projections in blindness (Cecchetti et al., 2016; Reislev et al., 2017), indicating that the increased FCs were based on strengthened structural connections (Messé, 2020; Peer et al., 2017; Shen et al., 2015). This mechanism can explain the increased FC between the somatosensory thalamus and high-level processing regions in blind individuals. Literature have reported strengthened structural connections between the thalamus and temporal regions (Marins et al., 2021). Another hypothesis to explain the increases in FC strength is the reorganization hypothesis (Cohen Kadosh and Walsh, 2006), which proposes that, due to postnatal experience, the thalamus might develop new connections to complete the relevant functions. Animal studies have provided direct evidence that congenital enucleation in rodents elicits the visual cortex to receive inputs from thalamic nuclei that are associated with the somatosensory and auditory cortices (Chabot et al., 2008; Karlen et al., 2006).

The GMV and FC analysis in our study can provide insights into the relation between GMV and FC; that is, the changes in FC are partly based on changes in the GMV of related brain regions, modulated by changes in the function of the related brain regions. Resting-state FC reflects synchronized neural activity without performance of a specific task (Greicius et al., 2003; Raichle and Mintun, 2006). This neural activity embodies the intrinsic function of brain regions. For example, the hub of information processing has strong FC with other regions, such as the thalamus (Crossley et al., 2013; Hwang et al., 2017), while injured regions have weak FC, such as the lesioned brain regions in post-stroke aphasia (Klingbeil et al., 2019). We postulate that there are at least four possible mechanisms of relationships between GMV and FC to interpret our findings. First, there are regions with reduced GMV induced by healthy neuronal degeneration (Terry et al., 1987) along with developed, improved functions accompanied by strengthened FC. For example, the GMVs in the somatosensory thalamus in blind children were higher, while the related FC was weaker than that of blind adults. The changes in GMV and FC with age were in line with previous studies (Fair et al., 2008; Hughes et al., 2012). Second, there were regions with reduced GMV induced by neuronal degeneration due to injury or input deprivation along with weakened function and FC. For example, the GMVs of visual cortical regions were lower in blind children, and their related FC was weaker than those in sighted children. Third, there were regions that had increased GMVs due to neuronal development and showed improved function and strengthened FC. Finally, there were regions that had no significant changes in GMV but showed improved function and strengthened FC. For example, the GMVs in the

somatosensory thalamus and visual cortical regions in blind adults were not significantly different from those in sighted adults, while the related functional connections in blind adults were significantly stronger than those in sighted adults. Further GMV-behavior correlation analysis showed that the somatosensory thalamus in blind adults was involved in high-level information processing, while it was not observed in sighted adults. This finding indicates that the changes in FC are partly based on the changes in GMV, but not in all cases. Further research is needed.

4.3. Functional reorganizations of the thalamus and visual cortical regions

In the human brain, there is a characteristic structure-to-function mapping, determined by extrinsic connections and intrinsic properties (Passingham et al., 2002). Distinct regions support distinctive functions, having preferred and nonpreferred sensory input modalities. For example, the primary auditory cortex preferentially processes information from the auditory modality, while the primary visual cortex preferentially processes information from the visual modality. An increasing number of studies have demonstrated that the structure and functions of the human brain can be modulated by external experience (Gudi-Mindermann et al., 2018; Matuszewski et al., 2021). Our study of blind individuals provides evidence for the functional plasticity of the brain. We found that the GMV values of the bilateral VL/VPL were significantly related to tactile verb generation in blind adults, whereas these regions are usually involved in primary tactile sensory perception in sighted individuals (Jones, 2012; Sherman and Guillery, 2001). Moreover, we did not find a significant correlation between these regions and the performance in tactile nonword reading, which involved more primary sensory information than the tactile verb generation task. These results indicate that functional reorganizations occur in the somatosensory thalamus. In addition, the somatosensory thalamus was reorganized to involve advanced language processing and did not merely stem from low-level aspects of somatosensory processing involved in Braille reading. These functional reorganizations in the bilateral VL/VPL can be interpreted in terms of the cognitive pluripotency theory (Bedny, 2017), which proposes that the cortical regions of the human brain are cognitively pluripotent and capable of supporting diverse cognitive functions at birth. Functional specialization is shaped by inputs and constrained by functional and structural connectivity as well as experience during development (Han et al., 2013; Li et al., 2020; Liu et al., 2021; Saygin et al., 2016). A large amount of somatosensory information input and the strengthened FCs with high-level information processing regions might influence the functional specialization of the bilateral VL/VPL.

Moreover, we found that the rVL/VPL-lCUN connection was significantly related to tactile nonword reading in blind children. This result suggests that functional reorganizations occurred in visual cortex. The lCUN engages in primary and high-level visual processing in sighted subjects (Bohrn et al., 2012; Palejwala et al., 2021; Price et al., 2005; Sun et al., 2011). However, the area involved in tactile processing in blind subjects. Therefore, blindness might cause the lCUN to undergo cross-modality reorganization. This is consistent with previous research, indicating that the visual cortical regions may be rewired to participate in nonvisual information processing when vision is absent and a large amount of somatosensory information is input (Beisteiner et al., 2015; Merabet et al., 2004).

In addition, we found that the FC between the somatosensory thalamus and the calcarine sulcus (lVL/VPL-rCS) was significantly related to visual verb generation in sighted children. This finding might be related to the development of the two nodes. The rCS in sighted individuals has been documented to subserve high-level language processing, such as lexical decision (Xiao et al., 2005), word reading (Van de Puttea et al., 2018), reading comprehension (Xia et al., 2018), and semantic typicality verification (Li et al., 2021). More importantly, the GVM values of the rCS were highest in sighted children relative to that in the other three groups (Fig. 3). This confirmed that childhood is the key period of rapid development of the brains of in sighted children, and some functions and structures might be pruned as years pass (Cao et al., 2014; Giedd et al., 1999). This finding might suggest that this node might have more active neurons in childhood. Hence, the FC of this node could profoundly reflect the relevance with the verb generation processing in children. With aging, the GMV values became low in sighted adults (Fig. 3), and was no longer relevant. Interestingly, we also found that the lVL/VPL was associated with the verb generation task in blind adults (Fig. 1B). This outcome is possibly because, due to plasticity, the long duration needed for learning braille enabled the somatosensory thalamus (lVL/VPL) to process advanced information. Therefore, the lVL/VPL was involved in the verb generation task in blind adults (Fig. 1B).

We also observed the FC of the somatosensory thalamus and the cuneus (rVL/VPL-lCUN) was significantly related to visual verb generation in sighted adults. It has been reported in the literature that the lCUN engages in high-level language processing in the sighted, such as word recognition (Sun et al., 2011), object naming (Price et al., 2005), and irony processing (Bohrn et al., 2012). Therefore, it is not surprising that the FC of to the node was associated with the verb generation task, although the GMV values of the node itself did not present a significant association with the task. We also found that the other node, rVL/VPL, was related to verb generation in blind adults (Fig. 1B). This result was possibly observed because learning braille involved the node in the process of high-level language. Moreover, our data show that the FC was correlated with the reading performance in blind children. This finding may also be related to the functional expansion of the rVL/VPL, possibly suggesting that cognitive reorganizations of rVL/VPL might occur in blind children.

4.4. Role of the thalamocortical pathway in nonvisual information processing in blind individuals

Previous studies have discovered that corticocortical pathways convey nonvisual information to occipital regions (Ioannides et al., 2013; Klinge et al., 2010), while some animal studies provided direct evidence that there might be thalamocortical pathways supporting tactile information processing (Chabot et al., 2008; Karlen et al., 2006). However, no direct evidence for thalamocortical pathways in humans has been reported. It is worth mentioning that Müller and colleagues (2019) reported indirect evidence for thalamocortical pathways in humans. They proposed a dual-route model of tactile information processing, that includes corticocortical and thalamocortical pathways in blindness. In the thalamocortical pathway, tactile information is first sent to the VP and VPL in the thalamus and then rerouted to the LGN, after which it is finally relayed to the primary visual area via the optic radiations. Our study provides direct evidence for anatomical thalamic rewiring in humans and strong supportive evidence for the role of the thalamocortical pathway. We observed that the GMV values of the VPL and LGN were significantly different between the blind and sighted groups, revealing atrophy of visual relay nuclei and hypertrophy of nonvisual relay nuclei in blind children. We also found that GMV values significantly increased from childhood to adulthood in the blind group, while they significantly decreased in the sighted group. These results provide supportive evidence that the VPL and LGN which may be part of the thalamocortical pathways might play an important role in the processing of nonvisual information. Moreover, we found that not only the somatosensory thalamus, visual thalamus and “visual” cortical regions but also the high-level information processing region contributed to nonvisual information processing in the blind.

4.5. Limitations

This study has at least the following caveates. 1) The children and adults participating in our study were different subjects at different ages. The distinct findings between these two groups might be a result of individual differences. 2) The number of congenitally blind children was small due to the difficulty of recruitment. 3) Fewer items in behavioral

tasks were used with the children than with the adults. Moreover, the tasks did not match well in input modality between sighted and blind groups. 4) The AAL atlas and BNA were used to divide the thalamus into regions. Thus, the regions defined in this study might not represent the true structural and functional differentiation of the thalamus. 5) The behavioral data were collected offline, and the brain-behavior correlations were not conducted in real time. 6) The ANOVA/ANCOVA treated the two independent variables (sex and age) as binary. This group division did not take into account the individual difference in age in each group. Future research should treated age as a continuous factor. Finally, 7) the current study focused on the cerebral profiles that showed significant interactions between vision and age factors. Future studies should further systematically analyze the main effects of these two factors.

5. Conclusion

The present study found that congenital blindness resulted in plastic changes in the thalamocortical network. The changes in the network included the “visual” and somatosensory regions in the thalamus. The structural volume of the visual thalamus in blind individuals, relative to that of sighted groups experienced a transformation from lower to higher between childhood and adulthood while that in the somatosensory thalamus in blind individuals experienced a transformation from higher than that of sighted individuals to not significantly different from that of sighted persons between childhood and adulthood. However, the connectivity strength of all thalamocortical connections underwent a transformation from weak to strong between blind childhood and blind adulthood. Moreover, the somatosensory thalamic regions and their functional connections with the visual cortical regions were reorganized to process high-level language tactile information in blind individuals. These findings may be related to the degeneration, development, and pluripotency of neurons.

Declaration of Competing Interest

The authors declare no competing financial interests.

Credit authorship contribution statement

Junfeng Lin: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Linjun Zhang:** Conceptualization, Investigation, Data curation. **Runhua Guo:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft. **Saiyi Jiao:** Data curation, Formal analysis. **Xiaomeng Song:** Data curation, Writing – original draft. **Suting Feng:** Data curation, Writing – original draft. **Ke Wang:** Data curation. **Mingyang Li:** Data curation. **Yudan Luo:** Data curation. **Zaizhu Han:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

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Supplementary materials

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References

Abboud, S., Cohen, L., 2019. Distinctive interaction between cognitive networks and the visual cortex in early blind individuals. Cereb. Cortex 29, 4725–4742. doi:10.1093/cercor/bhz006.

Aguirre, G.K., Datta, R., Benson, N.C., Prasad, S., Jacobson, S.G., Cideciyan, A.V., Bridge, H., Watkins, K.E., Butt, O.H., Dain, A.S., Brandes, L., Gennatas, E.D., 2016. Patterns of individual variation in visual pathway structure and function in the sighted and blind. PLoS One 11 (11), e0164677. doi:10.1371/journal.pone.0164677.

Amedi, A., Floel, A., Knecht, S., Zohary, E., Cohen, L.G., 2004. Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. Nat. Neurosci. 7 (11), 1266–1270. doi:10.1038/nn1328.

Ashburner, J., 2007. A fast diffeomorphic image registration algorithm. Neuroimage 38 (1), 95–113. doi:10.1016/j.neuroimage.2007.07.007.

Ashburner, J., Friston, K.J., 2001. Why voxel-based morphometry should be used. Neuroimage 14 (6), 1238–1243. doi:10.1006/nimg.2001.0961.

Barnes, J., Ridgway, G.R., Bartlett, J., Henley, S.M., Lehmann, M., Hobbs, N., Clarkson, M.J., MacManus, D.G., Ourselin, S., Fox, N.C., 2010. Head size, age and gender adjustment in MRI studies: a necessary nuisance? Neuroimage 53 (4), 1244–1255. doi:10.1016/j.neuroimage.2010.06.025.

Bathelt, J., Dale, N.J., De Haan, M., Clark, C.A., 2020. Brain structure in children with congenital visual disorders and visual impairment. Dev. Med. Child Neurol. 62 (1), 125–131. doi:10.1111/dmcn.14322.

Bavelier, D., Dye, M.W., Hauser, P.C., 2006. Do deaf individuals see better? Trends Cogn. Sci. 10 (11), 512–518. doi:10.1016/j.tics.2006.09.006.

Bedny, M., 2017. Evidence from blindness for a cognitively pluripotent cortex. Trends Cogn. Sci. 21 (9), 637–648. doi:10.1016/j.tics.2017.06.003.

Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., Saxe, R., 2011. Language processing in the occipital cortex of congenitally blind adults. Proc. Natl. Acad. Sci. U. S. A. 108 (11), 4429–4434. doi:10.1073/pnas.1014818108.

Bedny, M., Richardson, H., Saxe, R., 2015. "Visual" cortex responds to spoken language in blind children. J. Neurosci. 35 (33), 11674–11681. doi:10.1523/jneurosci.0634-15.2015.

Behrens, T.E., Johansen-Berg, H., Woolrich, M.W., Smith, S.M., Wheeler-Kingshott, C.A., Boulby, P.A., Barker, G.J., Sillery, E.L., Sheehan, K., Ciccarelli, O., Thompson, A.J., Brady, J.M., Matthews, P.M., 2003. Non-invasive mapping of connections between human thalamus and cortex using diffusion imaging. Nat. Neurosci. 6 (7), 750–757. doi:10.1038/nn1075.

Beisteiner, R., Windischberger, C., Geißler, A., Gartus, A., Uhl, F., Moser, E., Deecke, L., Lanzenberger, R., 2015. FMRI correlates of different components of Braille reading by the blind. Neurol. Psychiatry Brain Res. 21 (4), 137–145. doi:10.1016/j.npbr.2015.10.002.

Bohrn, I.C., Altmann, U., Jacobs, A.M., 2012. Looking at the brains behind figurative language-a quantitative meta-analysis of neuroimaging studies on metaphor, idiom, and irony processing. Neuropsychologia 50, 2669–2683. doi:10.1016/j.neuropsychologia.2012.07.021.

Bola, Ł., Siuda-Krzywicka, K., Paplińska, M., Sumera, E., Zimmermann, M., Jednoróg, K., Marchewka, A., Szwed, M., 2017. Structural reorganization of the early visual cortex following Braille training in sighted adults. Sci. Rep. 7 (1). doi:10.1038/s41598-017-17738-8, 17448-17448.

Boucard, C.C., Hernowo, A.T., Maguire, R.P., Jansonius, N.M., Roerdink, J.B.T.M., Hooymans, J.M.M., Cornelissen, F.W., 2009. Changes in cortical grey matter density associated with long-standing retinal visual field defects. Brain 132 (Pt 7), 1898–1906. doi:10.1093/brain/awp119.

Bridge, H., Cowey, A., Ragge, N., Watkins, K., 2009. Imaging studies in congenital anophthalmia reveal preservation of brain architecture in 'visual' cortex. Brain 132 (Pt 12), 3467–3480. doi:10.1093/brain/awp279.

Burton, H., Sinclair, R.J., Agato, A., 2012. Recognition memory for braille or spoken words: an fMRI study in early blind. Brain Res. 1438, 22–34. doi:10.1016/j.brainres.2011.12.032.

Cao, M., Wang, J.H., Dai, Z.J., Cao, X.Y., Jiang, L.L., Fan, F.M., Song, X.W., Xia, M.R., Shu, N., Dong, Q., Milham, M.P., Castellanos, F.X., Zuo, X.N., He, Y., 2014. Topological organization of the human brain functional connectome across the lifespan. Dev. Cogn. Neurosci. 7, 76–93. doi:10.1016/j.dcn.2013.11.004.

Cecchetti, L., Ricciardi, E., Handjaras, G., Kupers, R., Ptito, M., Pietrini, P., 2016. Congenital blindness affects diencephalic but not mesencephalic structures in the human brain. Brain Struct. Funct. 221 (3), 1465–1480. doi:10.1007/s00429-014-0984-5.

Chabot, N., Charbonneau, V., Laramée, M.E., Tremblay, R., Boire, D., Bronchti, G., 2008. Subcortical auditory input to the primary visual cortex in anophthalmic mice. Neurosci. Lett. 433 (2), 129–134. doi:10.1016/j.neulet.2008.01.003.

Chabot, N., Robert, S., Tremblay, R., Miceli, D., Boire, D., Bronchti, G., 2007. Audition differently activates the visual system in neonatally enucleated mice compared with anophthalmic mutants. Eur. J. Neurosci. 26 (8), 2334–2348. doi:10.1111/j.1460-9568.2007.05854.x.

Chabran, E., Noblet, V., Loureiro de Sousa, P., Demuynck, C., Philippi, N., Mutter, C., Anthony, P., Martin-Hunyadi, C., Cretin, B., Blanc, F., 2020. Changes in gray matter volume and functional connectivity in dementia with Lewy bodies compared to Alzheimer's disease and normal aging: implications for fluctuations. Alzheimers Res. Ther. 12 (1), 9. doi:10.1186/s13195-019-0575-z.

Cohen Kadosh, R., Walsh, V., 2006. Cognitive neuroscience: rewired or crosswired brains? Curr. Biol. 16 (22), R962–R963. doi:10.1016/j.cub.2006.10.017.

Crossley, N.A., Mechelli, A., Vértes, P.E., Winton-Brown, T.T., Patel, A.X., Ginestet, C.E., McGuire, P., Bullmore, E.T., 2013. Cognitive relevance of the community structure of the human brain functional coactivation network. Proc. Natl. Acad. Sci. U. S. A. 110 (28), 11583–11588. doi:10.1073/pnas.1220826110.

Damoiseaux, J.S., Greicius, M.D., 2009. Greater than the sum of its parts: a review of studies combining structural connectivity and resting-state functional connectivity. Brain Struct. Funct. 213 (6), 525–533. doi:10.1007/s00429-009-0208-6.
Debanne, D., Inglebert, Y., Russier, M., 2019. Plasticity of intrinsic neuronal excitability. Curr. Opin. Neurobiol. 54, 73–82. doi:10.1016/j.conb.2018.09.001.
Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., May, A., 2004. Changes in grey matter induced by training. Nature 427 (4972), 311–312. doi:10.1038/427311a.
Dukart, J., Bertolino, A., 2014. When structure affects function–the need for partial volume effect correction in functional and resting state magnetic resonance imaging studies. PLoS One 9 (12). doi:10.1371/journal.pone.0114227, e114227-e114227.
Fair, D.A., Cohen, A.L., Dosenbach, N.U., Church, J.A., Miezin, F.M., Barch, D.M., Raichle, M.E., Petersen, S.E., Schlaggar, B.L., 2008. The maturing architecture of the brain's default network. Proc. Natl. Acad. Sci. U. S. A. 105 (10), 4028–4032. doi:10.1073/pnas.0800376105.
Fan, F., Liao, X., Lei, T., Zhao, T., Xia, M., Men, W., Wang, Y., Hu, M., Liu, J., Qin, S., Tan, S., Gao, J.H., Dong, Q., Tao, S., He, Y., 2021. Development of the default-mode network during childhood and adolescence: a longitudinal resting-state fMRI study. Neuroimage 226, 117581. doi:10.1016/j.neuroimage.2020.117581.
Fan, L., Li, H., Zhuo, J., Zhang, Y., Wang, J., Chen, L., Yang, Z., Chu, C., Xie, S., Laird, A.R., Fox, P.T., Eickhoff, S.B., Yu, C., Jiang, T., 2016. The human brainnetome atlas: a new brain atlas based on connectional architecture. Cereb Cortex, 26 (8), 3508–3526. doi:10.1093/cercor/bhw157.
Forster, K.I., Forster, J.C., 2003. DMDX: a windows display program with millisecond accuracy. Behav. Res. Methods Instrum. Comput. 35 (1), 116–124. doi:10.3758/bf03195503.
Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S., Turner, R., 1996. Movement-related effects in fMRI time-series. Magn. Reson. Med. 35 (3), 346–355. doi:10.1002/mrm.1910350312.
Geier, K.T., Buchsbaum, B.R., Parimoo, S., Olsen, R.K., 2020. The role of anterior and medial dorsal thalamus in associative memory encoding and retrieval. Neuropsychologia 148, 107623. doi:10.1016/j.neuropsychologia.2020.107623.
Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., Paus, T., Evans, A.C., Rapoport, J.L., 1999. Brain development during childhood and adolescence: a longitudinal MRI study. Nat. Neurosci. 2 (10), 861–863. doi:10.1038/13158.
Goldszal, A.F., Davatzikos, C., Pham, D.L., Yan, M.X., Bryan, R.N., Resnick, S.M., 1998. An image-processing system for qualitative and quantitative volumetric analysis of brain images. J. Comput. Assist. Tomogr. 22 (5), 827–837. doi:10.1097/00004728-199809000-00030.
Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc. Natl. Acad. Sci. U. S. A. 100 (1), 253–258. doi:10.1073/pnas.0135058100.
Gudi-Mindermann, H., Rimmele, J.M., Nolte, G., Bruns, P., Engel, A.K., Röder, B., 2018. Working memory training in congenitally blind individuals results in an integration of occipital cortex in functional networks. Behav. Brain Res. 348, 31–41. doi:10.1016/j.bbr.2018.04.002.
Gupta, N., Ang, L.C., Noël de Tilly, L., Bidaisee, L., Yücel, Y.H., 2006. Human glaucoma and neural degeneration in intracranial optic nerve, lateral geniculate nucleus, and visual cortex. Br. J. Ophthalmol. 90 (6), 674–678. doi:10.1136/bjo.2005.086769.
Hamilton, R.H., Pascual-Leone, A., 1998. Cortical plasticity associated with Braille learning. Trends Cogn. Sci. 2 (5), 168–174. doi:10.1016/S1364-6613(98)01172-3.
Han, Z., Ma, Y., Gong, G., He, Y., Caramazza, A., Bi, Y., 2013. White matter structural connectivity underlying semantic processing: evidence from brain damaged patients. Brain 136 (Pt 10), 2952–2965. doi:10.1093/brain/awt205.
Heil, P., Bronchti, G., Wollberg, Z., Scheich, H., 1991. Invasion of visual cortex by the auditory system in the naturally blind mole rat. Neuroreport 2 (12), 735–738. doi:10.1097/00001756-199112000-00001.
Heine, L., Bahri, M.A., Cavaliere, C., Soddu, A., Laureys, S., Ptito, M., Kupers, R., 2015. Prevalence of increases in functional connectivity in visual, somatosensory and language areas in congenital blindness. Front. Neuroanat. 9, 86. doi:10.3389/fnana.2015.00086.
Huang, X., Wen, Z., Qi, C.X., Tong, Y., Dan, H.D., Xie, B.J., Shen, Y., 2020. Altered temporal dynamic intrinsic brain activity in late blindness. Biomed. Res. Int. 2020, 1913805. doi:10.1155/2020/1913805.
Hughes, E.J., Bond, J., Svrckova, P., Makropoulos, A., Ball, G., Sharp, D.J., Edwards, A.D., Hajnal, J.V., Counsell, S.J., 2012. Regional changes in thalamic shape and volume with increasing age. Neuroimage 63 (3), 1134–1142. doi:10.1016/j.neuroimage.2012.07.043.
Hwang, K., Bertolero, M.A., Liu, W.B., D'Esposito, M, 2017. The human thalamus is an integrative hub for functional brain networks. J. Neurosci. 37 (23), 5594–5607. doi:10.1523/jneurosci.0067-17.2017.
Ioannides, A.A., Liu, L., Poghosyan, V., Saridis, G.A., Gjedde, A., Ptito, M., Kupers, R., 2013. MEG reveals a fast pathway from somatosensory cortex to occipital areas via posterior parietal cortex in a blind subject. Front. Hum. Neurosci. 7, 429. doi:10.3389/fnhum.2013.00429.
Jenkinson, M., Beckmann, C.F., Behrens, T.E., Woolrich, M.W., Smith, S.M., 2012. FSL. Neuroimage 62 (2), 782–790. doi:10.1016/j.neuroimage.2011.09.015.
Jiang, A., Tian, J., Li, R., Liu, Y., Jiang, T., Qin, W., Yu, C., 2015. Alterations of regional spontaneous brain activity and gray matter volume in the blind. Neural Plast. 2015, 141950. doi:10.1155/2015/141950.
Jones, E.G., 2012. The Thalamus. Springer Science & Business Media.
Kafkas, A., Mayes, A.R., Montaldi, D., 2020. Thalamic-medial temporal lobe connectivity underpins familiarity memory. Cereb. Cortex 30 (6), 3827–3837. doi:10.1093/cercor/bhz345.
Kanjlia, S., Lane, C., Feigenson, L., Bedny, M., 2016. Absence of visual experience modifies the neural basis of numerical thinking. Proc. Natl. Acad. Sci. U. S. A. 113 (40), 11172–11177. doi:10.1073/pnas.1524982113.
Karlen, S.J., Kahn, D.M., Krubitzer, L., 2006. Early blindness results in abnormal corticocortical and thalamocortical connections. Neuroscience 142 (3), 843–858. doi:10.1016/j.neuroscience.2006.06.055.
Kim, J.S., Kanjlia, S., Merabet, L.B., Bedny, M., 2017. Development of the visual word form area requires visual experience: evidence from blind braille readers. J. Neurosci. 37 (47), 11495–11504. doi:10.1523/jneurosci.0997-17.2017.
Klingbeil, J., Wawrzyniak, M., Stockert, A., Saur, D., 2019. Resting-state functional connectivity: an emerging method for the study of language networks in post-stroke aphasia. Brain Cogn. 131, 22–33. doi:10.1016/j.bandc.2017.08.005.
Klinge, C., Eippert, F., Röder, B., Büchel, C., 2010. Corticocortical connections mediate primary visual cortex responses to auditory stimulation in the blind. J. Neurosci. 30 (38), 12798–12805. doi:10.1523/jneurosci.2384-10.2010.
Kral, A., Sharma, A., 2012. Developmental neuroplasticity after cochlear implantation. Trends Neurosci. 35 (2), 111–122. doi:10.1016/j.tins.2011.09.004.
Lein, E.S., Hawrylycz, M.J., Ao, N., Ayres, M., Bensinger, A., Bernard, A., Boe, A.F., Boguski, M.S., Brockway, K.S., Byrnes, E.J., Chen, L., Chen, L., Chen, T.M., Chin, M.C., Chong, J., Crook, B.E., Czaplinska, A., Dang, C.N., Datta, S., Dee, N.R., …, Jones, A.R., 2007. Genome-wide atlas of gene expression in the adult mouse brain. Nature 445 (7124), 168–176. doi:10.1038/nature05453.
Li, J.M., Bentley, W.J., Snyder, L.H., 2015. Functional connectivity arises from a slow rhythmic mechanism. Proc. Natl. Acad. Sci. U. S. A. 112 (19), E2527–E2535. doi:10.1073/pnas.1419837112.
Li, M., Song, L., Zhang, Y., Han, Z., 2021. White matter network of oral word reading identified by network-based lesion-symptom mapping. iScience 24 (8), 102862. doi:10.1016/j.isci.2021.102862.
Li, M., Xu, Y., Luo, X., Zeng, J., Han, Z., 2020. Linguistic experience acquisition for novel stimuli selectively activates the neural network of the visual word form area. Neuroimage 215, 116838. doi:10.1016/j.neuroimage.2020.116838.
Li, Q., Jiang, Q., Guo, M., Li, Q., Cai, C., Yin, X., 2013. Grey and white matter changes in children with monocular amblyopia: voxel-based morphometry and diffusion tensor imaging study. Br. J. Ophthalmol. 97 (4), 524–529. doi:10.1136/bjophthalmol-2012-302218.
Lingnau, A., Strnad, L., He, C., Fabbri, S., Han, Z., Bi, Y., Caramazza, A., 2012. Cross-modal plasticity preserves functional specialization in posterior parietal cortex. Cereb. Cortex 24 (2), 541–549. doi:10.1093/cercor/bhs340/JCerebralCortex.
Liu, Y., Shi, G., Li, M., Xing, H., Song, Y., Xiao, L., Guan, Y., Han, Z., 2021. Early top-down modulation in visual word form processing: evidence from an intracranial SEEG study. J. Neurosci. 41 (28), 6102–6115. doi:10.1523/jneurosci.2288-20.2021.
Liu, Y., Yu, C., Liang, M., Li, J., Tian, L., Zhou, Y., Qin, W., Li, K., Jiang, T., 2007. Whole brain functional connectivity in the early blind. Brain 130 (Pt 8), 2085–2096. doi:10.1093/brain/awm121.
Lövdén, M., Bäckman, L., Lindenberger, U., Schaefer, S., Schmiedek, F., 2010. A theoretical framework for the study of adult cognitive plasticity. Psychol. Bull. 136 (4), 659–676. doi:10.1037/a0020080.
Lu, T., Pan, Y., Kao, S.Y., Li, C., Kohane, I., Chan, J., Yankner, B.A., 2004. Gene regulation and DNA damage in the ageing human brain. Nature 429 (6994), 883–891. doi:10.1038/nature02661.
Macaluso, E., Frith, C.D., Driver, J., 2000. Modulation of human visual cortex by crossmodal spatial attention. Science 289 (5482), 1206–1208. doi:10.1126/science.289.5482.1206.
Marins, T.F., Russo, M., Rodrigues, E.C., Monteiro, M., Moll, J., Felix, D., Bouzas, J., Arcanjo, H., Vargas, C.D., Tovar-Moll, F., 2021. Reorganization of thalamocortical connections in congenitally blind humans. bioRxiv 449009. doi:10.1101/449009/JbioRxiv.
Matuszewski, J., Kossowski, B., Bola, Ł., Banaszkiewicz, A., Paplińska, M., Gyger, L., Kherif, F., Szwed, M., Frackowiak, R.S., Jednoróg, K., Draganski, B., Marchewka, A., 2021. Brain plasticity dynamics during tactile Braille learning in sighted subjects: multi-contrast MRI approach. Neuroimage 227, 117613. doi:10.1016/j.neuroimage.2020.117613.
Merabet, L., Thut, G., Murray, B., Andrews, J., Hsiao, S., Pascual-Leone, A., 2004. Feeling by sight or seeing by touch? Neuron 42 (1), 173–179. doi:10.1016/s0896-6273(04)00147-3.
Messé, A., 2020. Parcellation influence on the connectivity-based structure-function relationship in the human brain. Hum. Brain Mapp. 41 (5), 1167–1180. doi:10.1002/hbm.24866.
Müller, F., Niso, G., Samiee, S., Ptito, M., Baillet, S., Kupers, R., 2019. A thalamocortical pathway for fast rerouting of tactile information to occipital cortex in congenital blindness. Nat. Commun. 10 (1), 5154–5165. doi:10.1038/s41467-019-13173-7.
Newton, A.T., Rogers, B.P., Gore, J.C., Morgan, V.L., 2012. Improving measurement of functional connectivity through decreasing partial volume effects at 7 T. Neuroimage 59 (3), 2511–2517. doi:10.1016/j.neuroimage.2011.08.096.
Noppeney, U., Friston, K.J., Ashburner, J., Frackowiak, R., Price, C.J., 2005. Early visual deprivation induces structural plasticity in gray and white matter. Curr. Biol. 15 (13), R488–R490. doi:10.1016/j.cub.2005.06.053.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9 (1), 97–113. doi:10.1016/0028-3932(71)90067-4.
Pais-Roldán, P., Mateo, C., Pan, W.-J., Acland, B., Kleinfeld, D., Snyder, L.H., Yu, X., Keilholz, S., 2021. Contribution of animal models toward understanding resting state functional connectivity. Neuroimage 245, 118630. doi:10.1016/j.neuroimage.2021.118630.
Palejwala, A.H., Dadario, N.B., Young, I.M., O'Connor, K., Briggs, R.G., Conner, A.K., O'Donoghue, D.L., Sughrue, M.E., 2021. Anatomy and white matter connections of the lingual gyrus and cuneus. World Neurosurg. 151, e426–e437. doi:10.1016/j.wneu.2021.04.050.
Pan, W.J., Wu, G., Li, C.X., Lin, F., Sun, J., Lei, H., 2007. Progressive atrophy in the optic pathway and visual cortex of early blind Chinese adults: a voxel-based

morphometry magnetic resonance imaging study. Neuroimage 37 (1), 212–220. doi:10.1016/j.neuroimage.2007.05.014.
Pascual-Leone, A., Amedi, A., Fregni, F., Merabet, L.B., 2005. The plastic human brain cortex. Annu. Rev. Neurosci. 28, 377–401. doi:10.1146/annurev.neuro.27.070203.144216.
Passingham, R.E., Stephan, K.E., Kötter, R., 2002. The anatomical basis of functional localization in the cortex. Nat. Rev. Neurosci. 3 (8), 606–616. doi:10.1038/nrn893.
Peelle, J.E., Cusack, R., Henson, R.N., 2012. Adjusting for global effects in voxel-based morphometry: gray matter decline in normal aging. Neuroimage 60 (2), 1503–1516. doi:10.1016/j.neuroimage.2011.12.086.
Peer, M., Nitzan, M., Bick, A.S., Levin, N., Arzy, S., 2017. Evidence for functional networks within the human brain's white matter. J. Neurosci. 37 (27), 6394–6407. doi:10.1523/jneurosci.3872-16.2017.
Pell, G.S., Briellmann, R.S., Chan, C.H., Pardoe, H., Abbott, D.F., Jackson, G.D., 2008. Selection of the control group for VBM analysis: influence of covariates, matching and sample size. Neuroimage 41 (4), 1324–1335. doi:10.1016/j.neuroimage.2008.02.050.
Power, J.D., Mitra, A., Laumann, T.O., Snyder, A.Z., Schlaggar, B.L., Petersen, S.E., 2014. Methods to detect, characterize, and remove motion artifact in resting state fMRI. Neuroimage 84, 320–341. doi:10.1016/j.neuroimage.2013.08.048.
Price, C.J., Devlin, J.T., Moore, C.J., Morton, C., Laird, A.R., 2005. Meta-analyses of object naming: effect of baseline. Hum. Brain Mapp. 25, 70–82. doi:10.1002/hbm.20132.
Prins, D., Plank, T., Baseler, H.A., Gouws, A.D., Beer, A., Morland, A.B., Greenlee, M.W., Cornelissen, F.W., 2016. Surface-based analyses of anatomical properties of the visual cortex in macular degeneration. PLoS One 11 (1), e0146684. doi:10.1371/journal.pone.0146684.
Ptito, M., Herbin, M., Boire, D., Ptito, A., 1996. Neural bases of residual vision in hemicorticectomized monkeys. Prog. Brain Res. 112, 385–404. doi:10.1016/s0079-6123(08)63344-0.
Ptito, M., Schneider, F.C., Paulson, O.B., Kupers, R., 2008. Alterations of the visual pathways in congenital blindness. Exp. Brain Res. 187 (1), 41–49. doi:10.1007/s00221-008-1273-4.
Raichle, M.E., Mintun, M.A., 2006. Brain work and brain imaging. Annu. Rev. Neurosci. 29, 449–476. doi:10.1146/annurev.neuro.29.051605.112819.
Rauschecker, J.P., 1995. Compensatory plasticity and sensory substitution in the cerebral cortex. Trends Neurosci. 18 (1), 36–43. doi:10.1016/0166-2236(95)93948-W.
Reich, L., Szwed, M., Cohen, L., Amedi, A., 2011. A ventral visual stream reading center independent of visual experience. Curr. Biol. 21 (5), 363–368. doi:10.1016/j.cub.2011.01.040.
Reislev, N.H., Dyrby, T.B., Siebner, H.R., Lundell, H., Ptito, M., Kupers, R., 2017. Thalamocortical connectivity and microstructural changes in congenital and late blindness. Neural Plast. 2017, 9807512. doi:10.1155/2017/9807512.
Ricci, D., Anker, S., Cowan, F., Pane, M., Gallini, F., Luciano, R., Donvito, V., Baranello, G., Cesarini, L., Bianco, F., Rutherford, M., Romagnoli, C., Atkinson, J., Braddick, O., Guzzetta, F., Mercuri, E., 2006. Thalamic atrophy in infants with PVL and cerebral visual impairment. Early Hum. Dev. 82 (9), 591–595. doi:10.1016/j.earlhumdev.2005.12.007.
Rolls, E.T., Joliot, M., Tzourio-Mazoyer, N., 2015. Implementation of a new parcellation of the orbitofrontal cortex in the automated anatomical labeling atlas. Neuroimage 122, 1–5. doi:10.1016/j.neuroimage.2015.07.075.
Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012. The pulvinar regulates information transmission between cortical areas based on attention demands. Science 337 (6095), 753–756. doi:10.1126/science.1223082.
Sabbah, N., Authié, C.N., Sanda, N., Mohand-Saïd, S., Sahel, J.A., Safran, A.B., Habas, C., Amedi, A., 2016. Increased functional connectivity between language and visually deprived areas in late and partial blindness. Neuroimage 136, 162–173. doi:10.1016/j.neuroimage.2016.04.056.
Sadato, N., Okada, T., Honda, M., Yonekura, Y., 2002. Critical period for cross-modal plasticity in blind humans: a functional MRI study. Neuroimage 16 (2), 389–400. doi:10.1006/nimg.2002.1111.
Sato, W., Kochiyama, T., Uono, S., Sawada, R., Kubota, Y., Yoshimura, S., Toichi, M., 2019. Resting-state neural activity and connectivity associated with subjective happiness. Sci. Rep. 9 (1), 12098. doi:10.1038/s41598-019-48510-9.
Saygin, Z.M., Osher, D.E., Norton, E.S., Youssoufian, D.A., Beach, S.D., Feather, J., Gaab, N., Gabrieli, J.D., Kanwisher, N., 2016. Connectivity precedes function in the development of the visual word form area. Nat. Neurosci. 19 (9), 1250–1255. doi:10.1038/nn.4354.
Sbaihat, H., Rajkumar, R., Ramkiran, S., Assi, A.A.-N., Shah, N.J., Veselinović, T., Neuner, I., 2021. Dynamics of task-induced modulation of spontaneous brain activity and functional connectivity in the triple resting-state networks assessed using the visual oddball paradigm. PLoS One 16 (11), e0246709. doi:10.1371/journal.pone.0246709.
Shafiei, G., Markello, R.D., Makowski, C., Talpalaru, A., Kirschner, M., Devenyi, G.A., Guma, E., Hagmann, P., Cashman, N.R., Lepage, M., Chakravarty, M.M., Dagher, A., Mišić, B., 2020. Spatial patterning of tissue volume loss in schizophrenia reflects brain network architecture. Biol. Psychiatry 87 (8), 727–735. doi:10.1016/j.biopsych.2019.09.031.
Shen, K., Hutchison, R.M., Bezgin, G., Everling, S., McIntosh, A.R., 2015. Network structure shapes spontaneous functional connectivity dynamics. J. Neurosci. 35 (14), 5579–5588. doi:10.1523/JNEUROSCI.4903-14.2015.
Sherman, S.M., Guillery, R.W., 2001. Exploring the Thalamus. Academic Press.
Shimony, J.S., Burton, H., Epstein, A.A., McLaren, D.G., Sun, S.W., Snyder, A.Z., 2006. Diffusion tensor imaging reveals white matter reorganization in early blind humans. Cereb. Cortex 16 (11), 1653–1661. doi:10.1093/cercor/bhj102.
Shu, N., Li, J., Li, K., Yu, C., Jiang, T., 2009. Abnormal diffusion of cerebral white matter in early blindness. Hum. Brain Mapp. 30 (1), 220–227. doi:10.1002/hbm.20507.
Siuda-Krzywicka, K., Bola, Ł., Paplińska, M., Sumera, E., Jednoróg, K., Marchewka, A., Śliwińska, M.W., Amedi, A., Szwed, M. 2016. Massive cortical reorganization in sighted Braille readers. eLife, 5, e10762. https://doi.org/10.7554/eLife.10762
Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E., Johansen-Berg, H., Bannister, P.R., De Luca, M., Drobnjak, I., Flitney, D.E., Niazy, R.K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J.M., Matthews, P.M., 2004. Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage 23 (Suppl 1), S208–S219. doi:10.1016/j.neuroimage.2004.07.051.
Striem-Amit, E., Amedi, A., 2014. Visual cortex extrastriate body-selective area activation in congenitally blind people "seeing" by using sounds. Curr. Biol. 24 (6), 687–692. doi:10.1016/j.cub.2014.02.010.
Sullivan, E.V., Rosenbloom, M., Serventi, K.L., Pfefferbaum, A., 2004. Effects of age and sex on volumes of the thalamus, pons, and cortex. Neurobiol. Aging 25 (2), 185–192. doi:10.1016/s0197-4580(03)00044-7.
Sun, Y., Yang, Y., Desroches, A.S., Liu, L., Peng, D., 2011. The role of the ventral and dorsal pathways in reading Chinese characters and English words. Brain Lang. 119, 80–88. doi:10.1016/j.bandl.2011.03.012.
Tanaka, S., Kirino, E., 2017. Reorganization of the thalamocortical network in musicians. Brain Res. 1664, 48–54. doi:10.1016/j.brainres.2017.03.027.
Terry, R.D., DeTeresa, R., Hansen, L.A., 1987. Neocortical cell counts in normal human adult aging. Ann. Neurol. 21 (6), 530–539. doi:10.1002/ana.410210603.
Townsend, J.T., Ashby, F.G., 1983. *The Stochastic Modeling of Elementary Psychological Processes* (*Part 2*) Cambridge UP.
Tu, Y., Fu, Z., Mao, C., Falahpour, M., Gollub, R.L., Park, J., Wilson, G., Napadow, V., Gerber, J., Chan, S.-.T., Edwards, R.R., Kaptchuk, T.J., Liu, T., Calhoun, V., Rosen, B., Kong, J., 2020. Distinct thalamocortical network dynamics are associated with the pathophysiology of chronic low back pain. Nat. Commun. 11 (1), 3948. doi:10.1038/s41467-020-17788-z.
Uggetti, C., Egitto, M.G., Fazzi, E., Bianchi, P.E., Zappoli, F., Martelli, A., Lanzi, G., 1997. Transsynaptic degeneration of lateral geniculate bodies in blind children: in vivo MR demonstration. AJNR Am. J. Neuroradiol. 18 (2), 233–238.
Van de Putte, E., De Baene, W., Price, C.J., Duyck, W., 2018. Neural overlap of L1 and L2 semantic representations across visual and auditory modalities: a decoding approach. Neuropsychologia 113, 68–77. doi:10.1016/j.neuropsychologia.2018.03.037.
Wang, X., Caramazza, A., Peelen, M.V., Han, Z., Bi, Y., 2015. Reading Without Speech Sounds: VWFA and its Connectivity in the Congenitally Deaf. Cereb. Cortex 25 (9), 2416–2426. doi:10.1093/cercor/bhu044.
Wang, Y., Zuo, C., Wang, D., Tao, S., Hao, L., 2020. Reduced thalamus volume and enhanced thalamus and fronto-parietal network integration in the chess experts. Cereb. Cortex 30 (10), 5560–5569. doi:10.1093/cercor/bhaa140.
Wittenberg, G.F., Werhahn, K.J., Wassermann, E.M., Herscovitch, P., Cohen, L.G., 2004. Functional connectivity between somatosensory and visual cortex in early blind humans. Eur. J. Neurosci. 20 (7), 1923–1927. doi:10.1111/j.1460-9568.2004.03630.x.
Xia, Y., Xia, M., Liu, J., Liao, X., Lei, T., Liang, X., Zhao, T., Shi, Z., Sun, L., Chen, X., Men, W., Wang, Y., Pan, Z., Luo, J., Peng, S., Chen, M., Hao, L., Tan, S., Gao, J.-.H., Qin, S., Gong, G., Tao, S., Dong, Q., He, Y., 2022. Development of functional connectome gradients during childhood and adolescence. Sci. Bull. doi:10.1016/j.scib.2022.01.002.
Xia, Z., Zhang, L., Hoeft, F., Gu, B., Gong, G., Shu, H., 2018. Neural correlates of oral word reading, silent reading comprehension, and cognitive subcomponents. Int. J. Behav. Dev. 42, 342–356. doi:10.1177/0165025417727872.
Xiao, Z., Zhang, J.X., Wang, X., Wu, R., Hu, X., Weng, X., Tan, L.H., 2005. Differential activity in left inferior frontal gyrus for pseudowords and real words: an event-related fMRI study on auditory lexical decision. Hum. Brain Mapp. 25, 212–221. doi:10.1002/hbm.20105.
Yan, C.-.G., Cheung, B., Kelly, C., Colcombe, S., Craddock, R.C., Di Martino, A., Li, Q., Zuo, X.-.N., Castellanos, F.X., Milham, M.P., 2013. A comprehensive assessment of regional variation in the impact of head micromovements on functional connectomics. Neuroimage 76, 183–201. doi:10.1016/j.neuroimage.2013.03.004.
Yan, C.G., Wang, X.D., Zuo, X.N., Zang, Y.F., 2016. DPABI: data processing & analysis for (resting-state) brain imaging. Neuroinformatics 14 (3), 339–351. doi:10.1007/s12021-016-9299-4.
Yu, C., Shu, N., Li, J., Qin, W., Jiang, T., Li, K., 2007. Plasticity of the corticospinal tract in early blindness revealed by quantitative analysis of fractional anisotropy based on diffusion tensor tractography. Neuroimage 36 (2), 411–417. doi:10.1016/j.neuroimage.2007.03.003.
Zatorre, R.J., Fields, R.D., Johansen-Berg, H., 2012. Plasticity in gray and white: neuroimaging changes in brain structure during learning. Nat. Neurosci. 15 (4), 528–536. doi:10.1038/nn.3045.
Zhao, T., Liao, X., Fonov, V.S., Wang, Q., Men, W., Wang, Y., Qin, S., Tan, S., Gao, J.H., Evans, A., Tao, S., Dong, Q., He, Y., 2019. Unbiased age-specific structural brain atlases for Chinese pediatric population. Neuroimage 189, 55–70. doi:10.1016/j.neuroimage.2019.01.006.
Zhou, H., Schafer, R.J., Desimone, R., 2016. Pulvinar-cortex interactions in vision and attention. Neuron 89 (1), 209–220. doi:10.1016/j.neuron.2015.11.034.
Zhou, W., Pang, W., Zhang, L., Xu, H., Li, P., Shu, H., 2020. Altered connectivity of the visual word form area in the low-vision population: a resting-state fMRI study. Neuropsychologia 137, 107302. doi:10.1016/j.neuropsychologia.2019.107302.