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Altered connectivity of the visual word form area in the low-vision population: A resting-state fMRI study

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ABSTRACT

The present study investigated the resting-state functional connectivity (FC) of the visual word form area (VWFA) in low-vision people. Participants were 25 sighted and 37 low-vision individuals. During the experiment, participants underwent resting-state functional magnetic resonance imaging (rs-fMRI) scans. FC maps of the VWFA for sighted and low-vision participants were calculated separately and were contrasted with each other. Our results revealed a stronger FC between the VWFA and the inferior occipital cortex (IOC) but a weaker FC between the VWFA and the posterior central gyrus (PostCG) in the sighted people compared to the people with low vision. The region-of-interest-based analyses showed that the FC between the VWFA and PostCG in low-vision individuals who learned Braille was stronger relative to those who did not learn Braille, and that the FC between the VWFA and IOC was correlated with the onset age of Braille learning. These results suggest that the VWFA in people with low vision has a functional reorganization between visual and tactile processing, which was modulated by the experience of Braille reading.

1. Introduction

Neuroplasticity has been one of the central focuses in brain research. Sensory loss or cognitive training can induce both intramodal and cross-modal brain plasticity in adults (Herholz and Zatorre, 2012; Gougoux et al., 2009). The recent debates on brain training and cognition have further highlighted the importance of understanding the causal relationships between cognitive training and neuroplasticity (e.g., Malone et al., 2016). Previous research using functional magnetic resonance imaging (fMRI) and structural magnetic resonance imaging (sMRI) has consistently found evidence for cortical reorganization within the vision-related cortex of the blind, and showed that the reorganization impacts language processing, Braille reading, auditory processing, and tactile processing (see Beisteiner et al., 2015 and Hasson et al., 2016 for a review). Also, there can be cortical reorganization within vision-related cortex for the sighted people after training (Amedi et al., 2007; Kim and Zatorre, 2011; Power et al., 2012; Saito et al., 2006; Zangenehpour and Zatorre, 2010; Zangaladze et al., 1999).

The ventral visual cortex is organized through a hierarchical process starting from inferior occipital cortex (IOC) that processes simple visual features to higher-level visual regions in the inferior temporal cortex and fusiform that process more complex visual properties such as word forms (Felleman and Van Essen, 1991; Vinckier et al., 2007). While many studies on congenital blind people have focused on cortical reorganization within the occipital cortex (e.g., Butt et al., 2013, 2015; Liu et al., 2007; Striem-Amit et al., 2015), some researchers have investigated the cortical reorganization of higher-level visual regions such as the fusiform gyrus (e.g., Büchel et al., 1998a,b; Reich et al., 2011; Siuda-krzywicka et al., 2016; Striem-Amit and Amedi, 2014; Wang et al., 2015b). One important finding of these studies is that the left ventral occipito-temporal cortex (VOT), a classic region for visual word processing, is functionally connected to somatosensory cortices [i.e., posterior central gyrus (PostCG)] in sighted subjects after short periods of learning of Braille reading (Siuda-krzywicka et al., 2016). However, how the left

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VOT reorganizes its function for people with long-term visual deprivation has not been extensively examined. In the present study, we hope to disentangle the effects of visual deprivation from those of Braille reading experience on cortical reorganization for the left VOT, a region related to both vision and reading (McCandliss et al., 2003). Rather than examining congenitally blind people, all of whom can read and write in Braille, the present study examined low-vision people, only some of whom learn to read and write in Braille.

People with low vision perceive dimmer lights and feel it difficult or impossible to perform everyday tasks that require good vision. A number of studies revealed that visual deprivation alone would lead to superior tactile acuity (Kauffman et al., 2002; Goldreich and Kanics, 2003; Facchini and Aglioti, 2003; Sadato, 2005), while others claimed that this skill could be developed by training (Büchel et al., 1998a; Zeuner et al., 2002). Jednoróg and Grabowska (2008) found that there was a tactile sensitivity enhancement in low-vision individuals, especially in Braille readers, indicating that low-vision people may have undergone cortical reorganization for visual versus tactile functions.

For readers with normal vision, the left VOT has been found to be consistently engaged in word processing (McCandliss et al., 2003; Richlan et al., 2009; Shaywitz and Shaywitz, 2005; for reviews). Particularly, the middle region of the left VOT, the so-called visual word form area (VWFA), has been viewed as a hub for computing visual information (e.g., shape of letters) during word representation (McCandliss et al., 2003; Dehaene et al., 2010). The selectivity of the VWFA for word recognition may arise from a conjunction of two properties that make VWFA useful for reading: efficient reciprocal projections to language areas (Pinel and Dehaene, 2010) and a sensitivity to the visual features that characterize scripts, such as reliance on line junctions (Szwed et al., 2011), foveal position (Hasson et al., 2002), and high spatial frequencies (Woodhead et al., 2011).

Although many studies have confirmed the specialization of the VWFA for the visual representation of letters, growing evidence has shown that its specialization in either linguistic or visual processing is plastic. Dehaene et al. (2010) have demonstrated that the VWFA was engaged in word recognition in literate individuals, but this region was mainly engaged in face recognition rather than word recognition in illiterate people, suggesting that the linguistic specialization of the VWFA is shaped by reading experience. Recent research has proposed that the VWFA may be engaged in relative abstract processing (linking letter shapes to phonology) and is not necessarily dependent on visual sensory features (Striem-Amit et al., 2012). Siuda-krzywicka et al., 2016 have showed that visual word reading and tactile Braille reading activated similar locations in the VWFA for sighted people who learned Braille. Similarly, Burton et al.'s (2002) study has found that reading Braille activated vision-related cortex including the fusiform, and that congenitally blind participants differed from late blind participants in showing even greater activity in occipitotemporal cortex. Neuroimaging research on people with visual deprivation provides a good example for understanding the plasticity of the VWFA. As mentioned earlier, the recruitment low-vision people in the current study would help to disentangle whether the identified cortical reorganization can be attributed to visual deprivation or Braille reading experience.

While functional reorganization of an isolated region can be reflected by task-driven brain activation, resting-state functional connectivity (rs-FC) reveals the functional reorganization of an interested region, in a network perspective, through its altered associations with other regions. The rs-FC measures correlations of low-frequency Blood-Oxygenation-Level-Dependent (BOLD) signal fluctuations between local areas that are spontaneously activated at rest (Biswal et al., 1995), and the method can be used to explore the brain's intrinsic functional organization and examine if it is altered in neurological or psychiatric diseases (Friston, 2005; Koyama et al., 2010). Using this technique, previous studies of sighted people have found that the VWFA was functionally connected to ventral visual regions from occipital cortex to temporal cortex and to dorsal brain regions including the intraparietal sulcus (IPS), the frontal eye field (FEF) and the middle frontal gyrus (MFG) (Vogel et al., 2012; Zhou et al., 2015; Zhou et al., 2016). Furthermore, Siuda-krzywicka et al., 2016 has showed that following a tactile Braille learning course, the VWFA of sighted people increased its rs-FC with the somatosensory cortex while decreasing its coupling with other visual areas and the motor cortex. They also found a positive and significant correlation between functional connectivity of VWFA-somatosensory cortex and progress in tactile Braille reading speed after the course. These results suggest that the VOT could be recruited during tactile Braille reading in healthy adults with normal vision.

In sum, the present study aims to investigate the rs-FCs of the VWFA in low-vison individuals. Specifically, for people with low vision, our study attempts to address the following two question: 1) whether the VWFA is more correlated to vision-related cortex or other sensory cortices, and 2) whether the alterations of the FCs of the VWFA with other areas are due to deprivation of vision or experience in reading Braille. To answer the first question, we compared the FCs of the VWFA in sighted versus those of low-vision participants. If the function of VWFA is adapted for tactile processing, there would be evidence for enhancement of FCs between the VWFA and tactile related cortices. To answer the second question, we compared the FCs of VWFA in two subgroups within the low-vision participants, i.e., the group with or without Braille reading experience. In addition, the correlation between the FC strength of the VWFA and the onset time of Braille learning was calculated. If the cortical reorganization with the VWFA differs between sighted people and low-vision people who did not learn Braille, the change could be attributed to visual impairment or increase of general tactile experience; however, if the cortical reorganization differs between low-vision people who learned Braille versus those who did not, or if it is associated with the onset time of Braille learning, the change could be attributed to the learning experience with Braille.

2. Material and methods

2.1. Participants

Sixty-two students (M_{age} = 22 years, SD = ±3 years; 26 females) participated in this study. They were undergraduate or graduate students when tested. All students were native speakers of Chinese, and reported no hearing or learning disabilities. Individuals with a history of neurological diseases or psychiatric disorders were not recruited as our participants. The participants were divided into two groups: sighted (n = 25) and low-vision (n = 37). Within the low-vision group, they were further divided into two subgroups: 19 persons learned Braille and 18 persons did not. Low-vision individuals were recruited from the College of Special Education at the Beijing Union University. The diagnostic criterion, which defines low visual acuity as vision between 20/70 and 20/400 with the best possible correction, is based on WHO Collaborating Centers for Classification of Diseases (VII, Diseases of the eye and adnexa). Participants in each of these two groups were matched for age and gender (ps > .05). Table 1 shows the demographic data of participants. The study was approved by the Research Ethics Committee in the Department of Psychology at Peking University, and each participant signed an informed written consent before the experiment.

Table 1
Participants' demographic information and Braille learning experience.

	Sighted	Low vision	
		Learned Braille	Not learned Braille
Number of participants	25	19	18
Gender (male/female)	12/13	12/7	12/6
Age	22.8 (2.6)	22.2 (3.2)	22.3 (3.2)
Years of Braille learning	–	12.6 (4.3)	–

2.2. Imaging acquisitions and data preprocessing

MRI data were obtained on a SIEMENS PRISMA 3-T scanner in the Imaging Center for Brain Research at Peking University. We collected rs-fMRI data using an EPI sequence with the following parameters: EPI functional volumes = 240, axial slices = 64, thickness = 2 mm, in-plane resolution = 112 × 112, time of repetition = 2000 ms, time of echo = 30 ms, flip angle = 90°, field of view = 224 × 224 mm^2. During the resting-state session, the participants were instructed to remain motionless as much as possible and not to think actively about a particular idea with eye closed. T1-weighted image was also acquired for each participant with 192 contiguous sagittal slices of 1 mm thickness and 7° flip angle. Time of repetition was 2530 ms and time of echo was 2.98 ms. The acquisition matrix was 256 mm × 224 mm with voxel size of 1 × 1 × 1 mm^3.

Image preprocessing was carried out using the Data Processing Assistant for rs-fMRI pipeline analysis (DPARSF; Yan and Zang, 2010). For each participant, after converting the DICOM files to NIFTI images, the first 10 time points were discarded to allow for scanner stabilization and the subject's adaptation to the environment. The preprocessing on the remaining time points included: 1) slice timing for interleaved acquisitions, 2) a realigning step to correct for inter-scan head motions, 3) normalization of the functional images into the Montreal Neurological Institute (MNI) space by using T1 image unified segmentation and resampling to 2 × 2 × 2 mm^3, 4) spatial smoothing with a 4 mm FWHM Gaussian kernel, 5) nuisance correction by regressing out head motion using a Friston 24-parameter model (Friston et al., 1996) as well as individual white matter, cerebrospinal fluid and the global signals. 6) removal of the trend of time courses, and 7) temporal band-pass filtering (0.01–0.12 Hz). There was no group difference in the mean framewise displacement by accounting for head motion (Power et al., 2012), $F(2, 59) = 2.003$, $p = .819$.

2.3. FC analyses

We selected the seed centered on the coordinate of the classic VWFA (−45, −57, and −12 in MNI coordinates) (Cohen and Dehaene, 2004). For each subject, the resting-state time course was extracted for 4 mm spheres centered on the VWFA. The regional time course was calculated by averaging the time series of all of the voxels within the seed region. Then, the time course for each of the seed regions was correlated with every other voxel in the brain to generate individual seed maps (Fisher-r-to-z transformed). Finally, for each seed region, group-level analyses were performed: 1) One-sample t-tests for the seed maps of the sighted and low vision were conducted respectively; 2) Independent two-sample t-test between the seed maps of the sighted and low vision was conducted with the mask of Brodmann regions which contain voxels with positively significant FCs in one-sample t-tests. Whole-brain correction for multiple comparisons was performed using Gaussian Random Field Theory (Flitney and Jenkinson, 2000) at voxel $p < .001$ and cluster $p < .05$. The results were visualized using the template surface of smoothed ICBM152 in BrainNet Viewer (Xia et al., 2013).

In ROI-wise analyses, we focused on the function reorganization of the VWFA with respect to visual and tactile tasks. To avoid the issue of circular analysis (Kriegeskorte et al., 2009), we selected the seeds ($r = 4$ mm) in the somatosensory region (PostCG, MNI coordinate: 51 -35 54), and the vison region (IOC, MNI coordinate: 19 -96 -10) based on previous studies with tactile and visual tasks (Burton et al., 2002; Vinckier et al., 2007). The ROI-based FCs between the VWFA and the selected seeds were calculated respectively. Then we conducted one-way ANOVA for these FCs among sighted people, low-vision individuals who did not learn Braille [low vision (NB)], and low-vision individuals who learned Braille [low vision (B)]. In addition, to test whether there were altered FCs from the VWFA to non-sensory cortices, we calculated the FCs among the VWFA and two dorsal attention regions, the left MFG and IPS, which were selected according to Zhou et al. (2015). Finally, we specifically correlated the onset age of Braille learning with the strength of ROI-based FCs for the low-vision group. Given the *a priori* hypothesis about the ROI-based analysis, we used the least significant difference (LSD) method for multiple comparison correction.

3. Results

3.1. FCs from the VWFA for each group

Table 2 presents the areas that had significant FCs with the VWFA for the sighted group and the low-vision group, respectively. In both groups, the VWFA was positively connected to the bilateral prefrontal regions, superior parietal lobe, and visual regions extendeding from primary visual cortex to ventral occipitotemporal cortex.

3.2. Group difference in FCs of the VWFA

The regions showing stronger FC with the VWFA of the low-vision group relative to the sighted group (Fig. 1 and Table 1) included the left posterior central gyrus, bilateral parahippocampal gyrus and bilateral cuneus. The regions showing weaker FC with the VWFA of the low-vision group relative to the sighted group included the left inferior occipital cortex and superior frontal gyrus.

3.3. ROI-wise analyses

Results of ROI-based analyses (see Figs. 2 and 3) showed that there were positive FCs of VWFA-PostCG for sighted ($p = .024$), low vision

Table 2

Brain regions showing positively significant FC with VWFA for the sighted and low vision populations and the group difference.

MNI coordinate of peak value			Hemisphere	Brain region	Peak intensity
x	y	z			
Sighted					
−46	−56	−12	L	ITG/SPL	49.83
−24	−6	54	L	SFG	8.70
−50	8	34	L	IFG/MFG	8.41
−58	−2	−6	L	STG	6.05
52	−42	−20	R	ITG	9.85
28	−60	46	R	SPL	7.10
44	4	30	R	MFG	6.78
54	40	16	R	IFG	6.42
28	0	58	R	SFG	5.73
36	−82	18	R	MOC	5.00
Low-vision					
−46	−56	−12	L	ITG/SPL	51.11
−52	12	32	L	MFG	8.16
−28	−6	58	L	SFG	5.17
34	−70	−12	R	ITG/SPL	8.31
28	−2	50	R	SFG	6.12
42	34	12	R	IFG	5.83
22	−76	−46	R	CB	5.70
58	16	36	R	MFG	4.94
Low-vision > Sighted					
−16	−72	30	L	CUN	5.39
−22	−48	−6	L	PHG	4.82
−30	−34	60	L	PostCG	4.52
18	−42	−10	R	PHG	5.34
18	−66	14	R	CUN	4.99
Low-vision < Sighted					
−20	−94	−12	L	IOC	−4.29
−8	64	34	L	SFG	−4.28

Note. The results were corrected using Gaussian Random Field Theory (voxel $p < .001$, cluster $p < .05$, corrected). L = left, R = right. CB = cerebellum, CUN = cuneus, IFG = inferior frontal gyrus, IOC = inferior occipital cortex, ITG = inferior temporal gyrus, MFG = middle frontal gyrus, MOC = middle occipital cortex, PHG = parahippocampal gyrus, PostCG = posterior central gyrus, SFG = superior frontal gyrus, SPL = superior parietal lobe, STG = superior temporal gyrus.

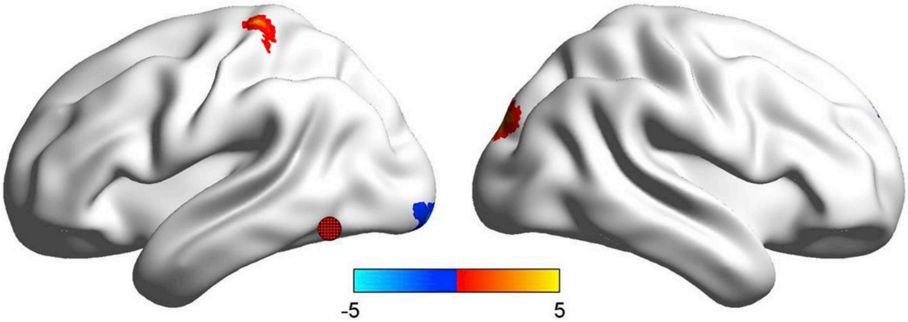

Fig. 1. Group difference in the VWFA seed maps. The map displays voxels showing significantly changed FCs in the low-vision group relative to the sighted group (voxel $p < .001$, cluster $p < .05$, corrected). The location of the seed is marked with a red and stripped sphere. The color bar denotes t-value. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

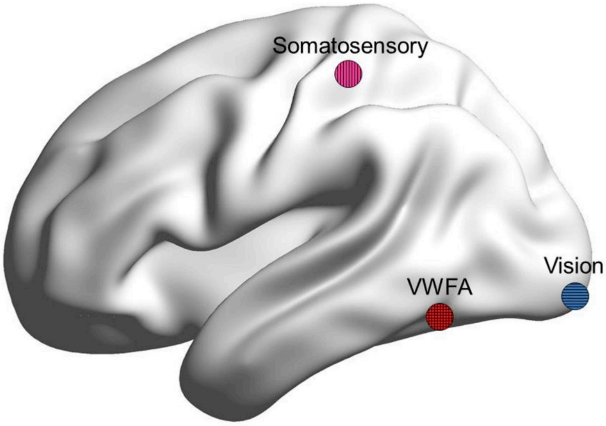

Fig. 2. Seeds selected for ROI-*wise* analyses.

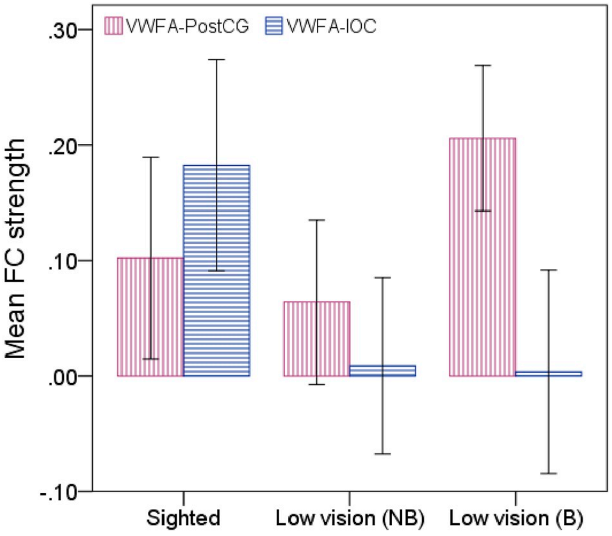

Fig. 3. ROI-based FCs of VWFA-PostCG and VWFA-IOC for sighted people (Sighted), low-vision individuals who did not learn Braille [Low vision (NB)], and low-vision individuals who learned Braille [Low vision (B)]. Error bar indicates 95% confidence interval. PostCG = posterior central gyrus. IOC = inferior occipital cortex. VWFA = visual word form area.

(NB) ($p = .069$), and low vision (B) groups ($p < .001$). The sighted group had a positively significant FC of VWFA-IOC ($p < .001$) while the other two groups did not ($ps > .05$). There was a significant interaction between groups [sighted, low vision (NB), low vision (B)] and FC type (somatosensory, vision) [$F(2,58) = 5.65$, $p = .006$], indicating different FC patterns among groups. The simple effect and post-hoc multiple comparisons showed that the FC strength of VWFA-PostCG was higher in individuals who learned Braille relative to those who did not learn Braille ($p = .014$) and sighted individuals ($p = .048$). The FC strength of VWFA-IOC was higher in sighted individuals relative to the low-vision individuals, regardless of whether they learned Braille ($p = .004$) or not ($p = .003$). In addition, we found that there were significant and positive FCs of VWFA-IPS, VWFA-MFG, and IPS-MFG ($ps < .05$) for each group, but there was no significant difference among groups ($ps > .05$). Zhou et al. (2015) also found significant FCs among the VWFA, IPS, and MFG, including significant differences in FCs of VWFA-MFG and IPS-MFG between dyslexic and control groups.

After conducting the correlations between the onset age of Braille learning and the strength of these ROI-wise FCs when age and gender were controlled, we found that the FC strength between the VWFA and the IOC decreased significantly with earlier onset time (or longer duration) of Braille learning ($r = 0.499$, $p = .03$; see Fig. 4). The correlations between the onset time of Braille learning and the FC strength of VWFA-PostCG was not significant ($p > .05$).

4. Discussion

Understanding how the visual cortex and related areas are remodeled by experience is a main focus in cognitive neuroscience research on neuroplasticity. In the present study, both whole brain analysis and ROI-

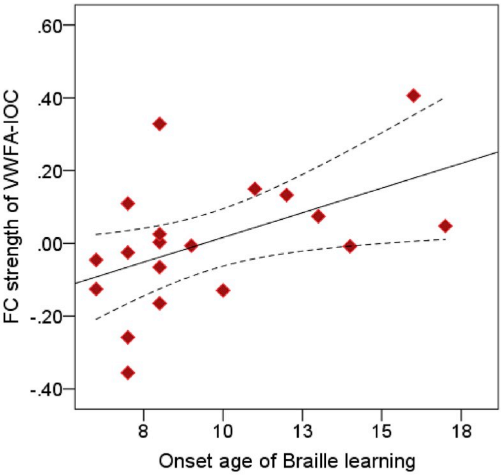

Fig. 4. Scatterplot of the correlation between the onset age (years) of Braille learning and the strength of FC between the VWFA and the inferior occipital cortex.

wise analysis showed that the sighted group had stronger FCs between the VWFA and the IOC but weaker FCs between the VWFA and the PostCG relative to the low-vision group. In addition, there was significant difference in the FC of VWFA-PostCG between the low-vision subgroups with and without Braille reading experience. In the subgroup with Braille reading experience, the FC strength between the VWFA and the IOC decreased significantly with earlier onset time (or longer duration) of Braille learning.

Previous studies showed that tactile Braille reading activated the VOT (e.g., Burton et al., 2002; Büchel et al., 1998a,b; Reich et al., 2011), the peak coordinate of which was similar to that of the VWFA for visual word recognition (Siuda-krzywicka et al., 2016). The present study used rs-FC to reveal cortical reorganization of the VWFA by testing the patterns of its associations with other regions. If the function of the VWFA is adapted for tactile word reading, there may be enhanced FCs between the VWFA and tactile related cortices. As expected, the FC between the VWFA and the somatosensory cortex increased and the FC between the VWFA and the primary visual cortex decreased for the low-vision group.

It is important to note that the difference between the sighted and low-vision subjects can be attributed to visual impairment or reliance on tactile sense in many everyday situations. The comparison between the low-vision subgroups with and without Braille reading experience could highlight the influence of Braille reading on neural reorganization. The results show that, on one hand, the adaption of FC between VWFA and IOC even existed in low-vision individuals who did not learn Braille and that there was no difference in the FC of VWFA-IOC between the two subgroups with low vision, suggesting that the cortical reorganization with the VWFA was initiated before any experience with Braille learning. In other words, the decreased FC between VWFA and IOC in low-vision individuals can be attributed to their decreasing reliance on visual sense or increasing reliance on non-verbal tactile sense in everyday situations. On the other hand, we found that 1) the FC between the VWFA and PostCG in low-vision individuals who learned Braille was stronger relative to those who did not learn Braille, and that 2) the FC between the VWFA and IOC was correlated with the onset age of Braille learning. These two pieces of evidence support that the cortical reorganization was also modulated by Braille reading experience within the Braille learners.

Why is there a convergence of visual and tactile reading in the VWFA? The study of Vogel et al. (2012) has found that the VWFA is functionally connected to many dorsal attentional regions such as IPS and dorsal prefrontal regions, which are involved in spatial processing. Both visual reading and tactile reading require spatial processing to analyze the shape of word and need visual attention to shift the reading from one word to another. In line with this argument, as indicated in the results of ROI-based analyses, both sighted and low-vision individuals have a network comprised of VWFA-IPS-MFG. Another explanation is that the VWFA is functionally connected to language-related areas such as the inferior frontal and inferior parietal regions. Relative to the FCs between the VWFA and the sensory-related cortices, the FCs between the VWFA and the regions for abstract linguistic processing are less likely influenced by visual deprivation. Consistently, the study of Wang et al. (2015a) found that the FCs with the VWFA between hearing and deaf people were very similar, except for the FC between the VWFA and the auditory speech area, indicating that the top-down modulation of the VWFA may arise from higher-order and modality-independent properties.

The group differences in FCs between the VWFA and the vision-related regions are complex. For the low-vision group as compared to the sighted group, although there was a weaker FC from the VWFA to IOC, stronger FCs from the VWFA to the parahippocampal gyrus and cuneus were observed. Previous researchers have showed that parahippocampal gyrus corresponds to selectivity for large objects and visual periphery representation (He et al., 2013; Levy et al., 2001; Striem-Amit et al., 2015). For sighted people, the IOC provides a basic visual input to the VWFA during visual word processing. For low-vision individuals, however, the parahippocampal gyrus may play a dominant role in processing large or rough visual input. Similarly, the enhanced FC between the VWFA and the cuneus in low-vision individuals may serve for spatial processing (Collignon et al., 2011; Sun et al., 2011) to compensate for degraded visual input. These results may be unique for low-vision individuals. It is noted that cortical reorganizations of vision-related cortices are different in subdivisions (e.g., Wang et al., 2015b), which should be examined in future studies.

In conclusion, we found that low-vision individuals and sighted people differ in the FCs between the VWFA and sensory cortical areas, but they have similar FCs between the VWFA and dorsal attention regions. These results reveal the functional reorganization of the VWFA for low-vision individuals and the modality-independent property of the VWFA in reading. More importantly, there was a difference in the FC of VWFA-PostCG between low-vision individuals who learned Braille versus those who did not. The FC between the VWFA and IOC becomes weaker with more Braille reading experience. These findings suggest that brain reorganization can be remodeled by the experience of Braille reading.

CRediT authorship contribution statement

Wei Zhou: Formal analysis, Writing - original draft, Writing - review & editing. **Wenbin Pang:** Investigation, Validation, Writing - original draft. **Linjun Zhang:** Conceptualization, Methodology, Resources. **Hongkai Xu:** Investigation. **Ping Li:** Writing - review & editing, Supervision. **Hua Shu:** Conceptualization, Writing - review & editing, Supervision, Project administration, Data curation.

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