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Neural network for Braille reading and the speech-reading convergence in the blind: Similarities and differences to visual reading

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ABSTRACT

All writing systems represent units of spoken language. Studies on the neural correlates of reading in different languages show that this skill relies on access to brain areas dedicated to speech processing. Speech-reading convergence onto a common perisylvian network is therefore considered universal among different writing systems. Using fMRI, we test whether this holds true also for tactile Braille reading in the blind. The neural networks for Braille and visual reading overlapped in the left ventral occipitotemporal (vOT) cortex. Even though we showed similar perisylvian specialization for speech in both groups, blind subjects did not engage this speech system for reading. In contrast to the sighted, speech-reading convergence in the blind was absent in the perisylvian network. Instead, the blind engaged vOT not only in reading but also in speech processing. The involvement of the vOT in speech processing and its engagement in reading in the blind suggests that vOT is included in a modality independent language network in the blind, also evidenced by functional connectivity results. The analysis of individual speech-reading convergence suggests that there may be segregated neuronal populations in the vOT for speech processing and reading in the blind.

1. Introduction

Reading is a process of decoding linguistic meaning from arbitrary symbols, which needs to be learned explicitly. Despite differences in the writing systems, the same neural reading network comprising of inferior frontal gyrus (IFG), precentral and supplementary motor areas, temporal linguistic areas of middle (MTG) and superior temporal gyri (STG), inferior parietal cortex and occipital areas, particularly the ventral occipitotemporal (vOT) cortex (Cohen et al., 2000; Dehaene and Cohen, 2011; Price and Devlin, 2003, 2011) - is activated by skilled adult readers (Rueckl et al., 2015).

The universal reading network largely overlaps with regions activated for speech perception (Rueckl et al., 2015). This effect, called speech-print convergence, was shown to emerge only after the acquisition of basic literacy skills (Chyl et al., 2018). These findings may explain why the neural correlates of reading are so astonishingly similar between different writing systems. The neural network for spoken language processing is considered universal for humankind, as it is evolutionary old (Kirby, 2007). All writing systems encode spoken language and thus the reading network most likely develops by encompassing the language network. It was argued that speech-reading convergence (we will use term speech-reading convergence from now on as it is less tied to specific modality used for reading than the term speech-print convergence) is a universal principle of brain organization resulting from the biological constraints imposed by perisylvian specialization for speech, and the need to use these specialized systems for written language comprehension (Rueckl et al., 2015).

Studying sensory deprivation enables exploring the limits of the astonishing universality of the neural correlates of reading (Ricciardi et al., 2014). Though blind subjects use the same modality for spoken language processing as the sighted ones, Braille readers deploy the sense of touch and not vision for reading Braille (Braille, 1839). The neural network for spoken language processing resides in very similar regions in the blind and in the sighted (Röder et al., 2002). The most significant difference is the involvement of the occipital cortex in speech processing (Burton et al., 2003, Bedny et al., 2011) in the blind subjects. The vOT cortex was also shown to be active during speech processing being sensitive to syntactical information in the blind but not in the sighted (Kim et al., 2017).

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Table 1
Participants of the study, age and the age of blindness onset given in years.

Blind subjects							Sighted subjects			
Subject	Age	Sex	Handedness	Blindness onset	Cause of blindness	Reading Hand	Subject	Age	Sex	Handedness
B1	35.45	F	R	0	Unknown	R	S1	30.24	F	R
B2	36.36	F	R	0	Retinopathy of prematurity	L	S2	44.66	F	R
B3	30.29	F	R	0	Retinopathy of prematurity	L	S3	45.41	F	R
B4	44.13	F	R	0	Congenital rubella syndrome	R	S4	30.56	F	R
B5	47.96	F	R	0	Unknown	L	S5	19.68	F	R
B6	36.85	F	R	0	Glaucoma	R	S6	37.59	F	R
B7	31.02	F	R	0	Leber's congenital amaurosis	R	S7	24.09	F	R
B8	18.99	F	R	2	Retinoblastoma	R	S8	41.76	F	R
B9	27.78	F	R	0	Leber's congenital amaurosis	L	S9	37.48	F	R
B10	38.70	F	R	3	Mechanical damage	R	S10	59.83	F	R
B11	41.70	F	R	0	Retinopathy of prematurity	R	S11	37.64	F	R
B12	60.32	F	R	0	Retinopathy of prematurity	R	S12	26.92	F	R
B13	41.30	F	R	0	Leber's congenital amaurosis	R	S13	41.83	F	R
B14	24.03	F	R	0	Congenital rubella syndrome	R	S14	28.34	F	L
B15	28.21	F	L	0	Optic nerve hypoplasia	R	S15	45.74	F	R
B16	45.18	F	R	0	Retinopathy of prematurity	L	S16	36.63	F	R
B17	37.84	M	R	0	Optic nerve hypoplasia	R	S17	21.74	M	R
B18	46.10	M	R	0	Optic nerve hypoplasia	L	S18	35.27	M	R
B19	35.74	M	R	0	Unknown	L	S19	27.87	M	R
B20	21.00	M	R	0	Retinopathy of prematurity	L	S20	33.65	M	R
B21	37.76	M	R	0	Retinitis pigmentosa	R	S21	38.05	M	R
B22	52.43	M	R	0	Cataract, glaucoma	L	S22	32.15	M	R
B23	19.39	M	R	0	Bilateral microphthalmia	L	S23	36.07	M	R
B24	27.06	M	R	0	Retinopathy of prematurity	R	S24	19.10	M	R
B25	36.18	M	R	0	Retinopathy of prematurity	L	S25	52.27	M	R

With respect to Braille reading, only few studies focused on the areas outside the occipital cortex (Büchel et al., 1998, Burton et al., 2012). It was shown that single word recognition in Braille activates the left inferior frontal gyrus (Büchel, Price, and Friston, 1998) and the vOT cortex closely corresponding to the area activated by reading in the sighted subjects (Büchel et al., 1998, Burton et al., 2012). Reich and colleagues (2011) found that the location of the activation specific to reading in the vOT cortex is practically identical in the blind and in the sighted, both on group and individual levels. As detailed characterisations of the reading network and speech-reading convergence in the blind are still lacking, we decided to test whether the universality of the reading network and speech-reading convergence extends across modalities.

We predicted that visual and Braille reading neural networks should largely overlap in classical areas (left vOT, temporal linguistic areas, IFG), as suggested by the previous literature (Büchel, Price, and Friston, 1998; Reich et al., 2011). The differences were expected in the occipital and somatosensory cortex, where we anticipated activation related to Braille, but not visual reading. Additionally, as the previous literature has shown that the speech processing networks of the blind and of the sighted are largely similar (Röder et al., 2002), we hypothesized that speech-reading convergence would be similar in the two groups and would be present, as in the sighted population (Rueckl et al., 2015), in perisylvian brain regions.

2. Materials and methods

2.1. Participants

Twenty-five blind (mean age: 35.71, age SD: 10.08, 16 females) and 25 sighted (mean age: 35.42, age SD: 9.68, 16 females) subjects participated in the study (Table 1). All of the blind subjects had at most minimal light perception (12 subjects, measured by a questionnaire, see Supplementary Material). The blind subjects began to learn Braille between the age of 6 and 9 and assessed their ability to read Braille as average, good or very good. Only one participant judged her Braille skills as weak, however, her reading performance (words read per minute) was similar to the rest of the blind group (behavioural results are presented in the Supplementary Materials). None of the participants had any history of neurological illness or brain damage (other than the cause of blindness) and all of the participants declared having normal hearing. All of the anatomical images were assessed by a radiologist and no brain damage was found in any of the subjects. Handedness was measured using Edinburgh Handedness Questionnaire translated to Polish. Almost all of the participants were right handed (one left-handed participant in the blind group and one in the sighted group). Twelve of the blind subjects used non-dominant hand for Braille reading (11 left, 1 right). As the onset of blindness can alter the functional organization of the brain (Burton et al., 2002, Bedny et al., 2012), we have conducted the analyses with and without the two subjects that lost their sight after birth (presented in Supplementary Materials). As the differences were minor, we report the whole-sample results.

2.2. fMRI task and procedure

During the MRI session participants completed multiple tasks and structural scans. Here we are analysing only the fast language localizer task (Malins et al., 2016, Chyl et al., 2018). In this localizer task, subjects were presented with auditory and tactile (blind group) or auditory and visual (sighted group) stimuli in three conditions – real words, pseudowords and non-linguistic control (Fig. 1). The task was to read and listen to the stimuli and was programmed using Presentation software (Neurobehavioral Systems, Albany, CA).

Auditory stimuli were presented via noise-attenuating headphones (NordicNeuroLab), visual stimuli were displayed on an LCD monitor, while tactile stimuli via NeuroDevice Tacti^{TM} Braille display (Debowska et al., 2013). Real words were balanced between conditions in the number of adjectives, verbs and nouns of similar frequency (Fiebach et al., 2002). Stimuli were short (3-4 letters) and consisted of 1 or 2-syllables. Pronounceable pseudowords were created to be as similar as possible to the real words, by transposition or substitution of letters. Visual non-linguistic control stimuli consisted of 3-4 hashtags, tactile non-linguistic control stimuli consisted of 3-4 six-dots symbols (unmeaningful Braille sign in Polish). Auditory non-linguistic control stimuli were 1 or 2-syllable words (in order to match real and pseudowords length) vocoded using Praat (www.praat.org). This process di-

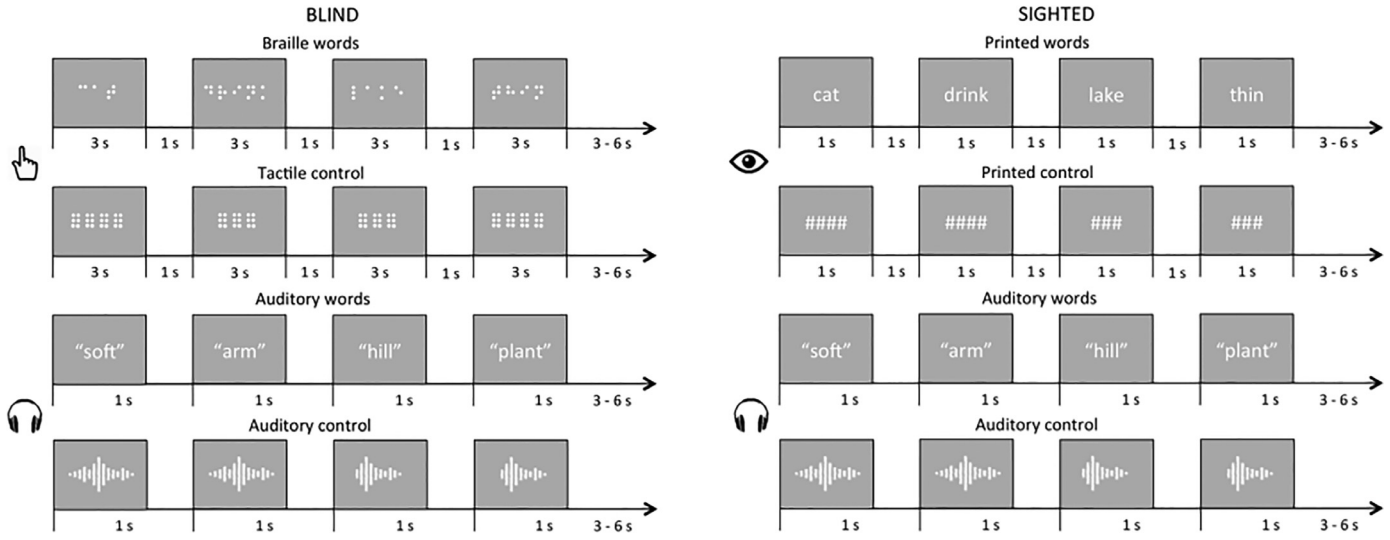

Fig. 1. Experimental design and fMRI task overview, Braille words, pseudowords and control stimuli (six dots Braille sign - symbol without linguistic meaning in Polish Braille) presented tactually, printed words, pseudowords and control stimuli (hash symbols) presented on the screen, auditory stimuli (words, pseudowords and vocoded words) presented in headphones.

vides the speech signal into 3 frequency bands, applies the dynamic amplitude contour of the original to a noise source, then recombines these into a unitary signal again. This results in an auditory stimulus that retains the same dynamic frequency and amplitude pattern of the original, but largely destroys phonetic content.

The task was presented in three runs. Each run consisted of 36 blocks – 18 auditory and 18 tactile or visual including 6 blocks per condition (real words, pseudowords and non-linguistic control). Within each block, four different stimuli from the same condition were presented in succession. Auditory and visual stimuli were displayed for 1000 ms, while tactile stimuli were displayed for 3000 ms (Kim et al., 2017, Veispak et al., 2012) with 1000 ms interstimulus interval. Blocks were separated with 3000 to 6000 ms breaks.

2.3. fMRI acquisition

The data were obtained on the 3T Siemens Trio Scanner. The functional images were acquired in a whole-brain echo-planar imaging (EPI) sequence with 12 channel head coil (32 slices, slice-thickness = 4 mm, TR = 2000 ms, TE = 30 ms, flip angle = 80°, FOV = 200 mm^3, matrix size = 64 × 64, voxel size: 3.4 × 3.4 × 4 mm). The anatomical images were acquired using T1-weighted (T1w) MPRAGE sequence with 32 channel head coil (176 slices, slice-thickness: 1 mm, TR = 2530 ms, TE = 3.32 ms, flip angle = 7°, matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm).

2.4. Whole-brain analyses

Preprocessing and statistical analyses were conducted in SPM 12 (SPM12, Wellcome Trust Centre for Neuroimaging, London, UK) running on Matlab2017b (The Math-Works Inc. Natick, MA, USA) and in SPSS 25. The standard preprocessing pipeline was applied. Firstly, all of the functional data were realigned to the mean functional image. The anatomical images were then coregistered to the mean functional image and segmented based on the template provided in SPM. Afterwards, the normalization of the functional data to the MNI space was carried out with voxel size 2 × 2 × 2 mm. Finally, images were smoothed with an 8 mm isotropic Gaussian kernel.

Preprocessed data were analysed using a voxel-wise GLM approach. The ART toolbox (https://www.nitrc.org/projects/artifact_detect) was additionally used to create movement regressors as well as to detect the excessive in-scanner motion – movement over 1.6 mm and rotation over 0.04 mm in relation to the previous volume (around half of the voxel size, Kowalski et al., 2019). In order to include a session in the analyses, 80% of the volumes needed to be artefact free. None of the sessions were rejected. The blocks of six conditions were convolved with canonical haemodynamic function.

Reading related activations were studied using two different contrasts. Word sensitive (words > baseline, baseline understood as unmodeled rest) contrast was used to delineate brain regions sensitive to reading, thus including areas involved in sensory processing of the stimuli. Word specific (words > non-linguistic control stimuli) contrast was used to look for regions specifically engaged in the processes of reading – not only processing physical characteristics of the perceived stimuli, but involved in higher-order, purely linguistic processes. Both contrasts were used in the reading research (Martin et al., 2015) and words > baseline contrast was specifically employed in the studies focusing on the speech-reading convergence in adults (Rueckl et al., 2015), as well as in children (Chyl et al., 2018, Chyl et al., 2021, Marks et al., 2019, Preston et al., 2016). Within group results were computed using one sample t-tests with first level contrast images as input. In order to compare automatic whole-word reading and serial reading-related activations, the pseudowords > words first-level contrasts were also computed using one-sample t-test within each group. Conjunction analysis approach (null conjunction, Friston et al., 2005) was employed to look for regions common for visual and Braille reading networks between groups. Additionally, to account for individual differences in the location of the reading sensitive activation we conducted individual peak analyses as described in the Reich et al. (2011) study (see Supplementary Materials for more details). Second level two-sample *t*-tests were used for the direct comparisons of the blind and sighted groups. Whole-brain analyses were thresholded at voxel level at $p < 0.001$, cluster corrected at FWE $p < 0.05$. To avoid results produced by differences in de-activation, the neurobiological basis of which remains unknown (Frankenstein et al., 2003), all group level results were masked by an image of positive activations (sum of activation for all conditions in both groups, at voxel level $p < 0.05$). The anatomical regions were identified according to AAL3 atlas (Rolls et al., 2020) and the structures contributing more than 50 voxels to the clusters are described in the tables.

2.5. Speech-reading convergence

In order to study the speech-reading convergence in both groups, we applied two different analytic approaches: intersect maps for reading and speech processing on the whole brain and individual convergence analysis in selected regions of interest (ROIs). Whole-brain conjunction analyses were used in order to estimate the intersect between the reading and speech sensitive activations (words > baseline, Rueckl et al., 2015). In the individual convergence analysis we used two measures - number of voxels in the individual convergence maps and correlation of the reading sensitive and speech sensitive contrasts estimates (Chyl et al., 2018, Chyl et al., 2021, Marks et al., 2019, Preston et al., 2016).

It was our goal to conduct the analyses in the way comparable with previous studies on speech-reading convergence in the sighted population (adults - Rueckl et al. 2015, children - Preston et al. 2016, Chyl et al., 2018, Chyl et al., 2021, Marks et al. 2019). All of these studies, despite different tasks employed (semantic decision - Rueckl et al., 2015; passive observation - Chyl et al., 2018, Chyl et al., 2021); word matching - Marks et al., 2019; word-picture identification task - Preston et al., 2016) compared experimental reading and speech conditions to rest and not to different control conditions and then examined the convergence by the means of conjunction between these contrasts. In our study we applied a similar approach, however, to control for the effects of multisensory processing, we report the conjunctions of the language specific conditions (words > non-linguistic control) in the Supplementary Materials (Table S10, Figure S5).

On the individual level, analyses were conducted in literature-based ROIs. The ROIs were created as spheres of 10 mm radius around the peaks of activations reported by Rueckl and colleagues (2015) as areas that have shown both speech-reading convergence and significant correlation of reading and speech processing estimates. They were localized in left IFG/precentral gyrus, right STG, left MTG/STG, left IFG and left inferior parietal lobule (Table 1 in Rueckl et al. (2015), left insula, anterior cingulate and left thalamus peaks were outside the activation mask and thus were not considered). Additionally, the bilateral vOT ROIs were tested, as this region was previously reported to be sensitive to speech processing (Kim et al., 2017) and it was present in the speech-reading conjunction in the blind group in the whole-brain analyses. The vOT ROIs were created as combined 10 mm spheres around the peaks of activation: LEX peak from the Lerma-Usabiaga et al., (2018) study and the peak of the vOT activation of aurally presented words in a blind sample from the Kim et al. study (2017). The left hemisphere vOT ROI was flipped onto the right hemisphere. All of the ROIs were inspected for the number of voxels overlapping between the reading and speech processing activations (described below). In several ROIs (left IFG/precentral gyrus, left IFG, left inferior parietal lobule) more than 40% of participants in either of the groups had no overlap between reading and speech processing activations. These ROIs were not considered for further analyses. The majority of sighted participants also did not show the overlap in the left and right vOT ROIs. The left vOT ROI was still analysed as it was of particular interest. Finally, three ROIs were selected for the individual convergence analysis: right STG, left MTG/STG, and left vOT.

For each subject, the binary map of conjunction between reading and speech sensitive activations (words > baseline) was created using the $p < 0.05$ null conjunction threshold (conjoint probability $p < 0.0025$; Chyl et al., 2021, Preston et al., 2016, Marks et al., 2019). The number of voxels significantly activated for such conjunction was calculated for each subject in the ROIs. Additionally, to control for the relative degree of brain activation for each condition, the number of voxels activated at $p < 0.05$ in the positive activation mask (used for masking of the whole-brain results) was calculated for each participant. The standardized residuals of the regression analysis with the number of the overlapping voxels in a given ROI as the dependent variable and the degree of general individual activation for reading and speech processing as predictors were analysed. The Mann-Whitney U test was used to test for group differences and all of the *p*-values were corrected for multiple comparisons using Bonferroni-Holm correction.

Secondly, the same ROIs (right STG, left MTG/STG and left vOT) were used in the analysis of the correlation between reading and speech sensitive activations. From each ROI the contrast estimate for the given condition (written and spoken words > baseline contrast) was extracted in each subject using MarsBar toolbox (version 0.44, Brett et al., 2002). Individual subjects' measures were then introduced into correlation analysis using the Spearman's rho correlation coefficient. The correlation coefficients were compared between the groups using Fisher's r to z transformation (Armitage and Colton, 2005). All of the p-values were corrected for multiple comparisons using Bonferroni-Holm correction.

The left vOT area turned out to be the main region of the speech-reading convergence in the blind group on the group level. Thus, in a post-hoc manner, the individual overlaps between reading and speech specific activity in the vOT were calculated in this group following the methodology presented by Planton et al., (2019). The reading and speech specific (word > non-linguistic control contrasts) individual ROIs were defined as voxels significantly active (individual maps thresholded at $p < 0.001$) in the volume of search (sum of the group-level vOT clusters from reading and speech specific contrasts, $p < 0.001$, FWE cluster corrected $p_{cluster} < 0.05$). The overlapping voxels between the reading and speech specific individual ROIs were counted for each subject.

Also following Planton et al. (2019), the activity during speech processing in the vOT voxels activated during reading was tested. For every subject an individual reading-related ROI was defined as voxels that were significantly activated by the reading specific contrast (words > non-linguistic control, individual activation maps thresholded at $p < 0.001$, uncorrected) in the volume of search (left vOT activations on the group level, $p < 0.001$, FWE cluster corrected $p_{cluster} < 0.05$). The speech specific contrast estimates (words > non-linguistic control) were extracted from the individual ROIs. The Wilcoxon signed-rank test was used to assess whether the speech-related activations were significantly different from zero.

2.6. Functional connectivity analyses

Task-related functional connectivity with a seed-to-voxel correlation mapping (weighted GLM option) was performed using the CONN Toolbox v.19 (Whitfield-Gabrieli and Nieto-Castanon, 2012). Spatial normalization of the structural data was conducted in the toolbox, as well as default denoising procedure (combination of aCompCor, regressing out excessive movement, motion regression, main effect of task regression) of the functional data, preprocessed as described above. The functional data were high-pass filtered (0.008 Hz, as recommended by the toolbox developers for the task-related connectivity analyses). White-matter, grey-matter and cerebrospinal fluid signals and BOLD signal standard deviation (after denoising) were entered as nuisance second-level covariates to GLM. The left vOT ROI, described above was used as seed. Second-level results of within and between groups comparisons of the task-related correlations thresholded at $p < 0.001$, FWE cluster corrected $p_{cluster} < 0.05$ are reported. As functional connectivity analysis is complementary to the functional activations' analyses, we focus only positive correlations, omitting negative correlations of which interpretation could be unclear.

2.7. Data availability

Behavioural, individual subject analyses data and second level data are available online (https://osf.io/uqv8s/).

2.8. Ethics statement

The study was approved by the Scientific Studies Ethics Committee of the Institute of Psychology, Jagiellonian University applying The Declaration of Helsinki rules. Subjects signed an informed consent form

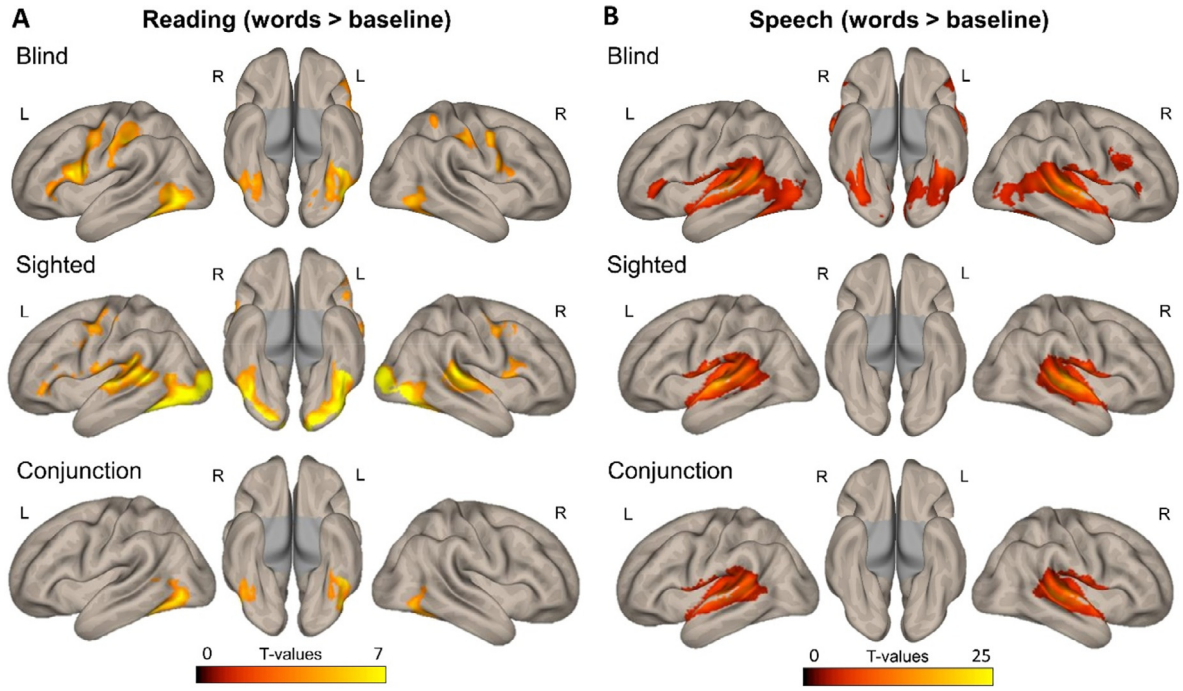

Fig. 2. A) Reading and B) speech sensitive (word > baseline) activations in blind and sighted participants together with group conjunctions, L – left hemisphere, R – right hemisphere. All contrasts at voxelwise $p < 0.001$ and cluster wise $p < 0.05$ FWE corrected.

at the beginning of the experimental session. The form was sent to the blind subjects beforehand in a format readable by the screen reading software.

3. Results

3.1. Similarities and differences between the language networks in the blind and in the sighted

Reading sensitive activations (words > baseline) were present in the areas typically associated with the reading network (bilateral: vOT, precentral/postcentral gyri, IFG) in both the sighted and the blind (Fig. 2A, Table 2). The regions of the significant conjunction between Braille and visual reading sensitive networks were found in the bilateral vOT. For this contrast, the blind subjects activated bilateral occipital clusters (loci of V1/V2) as well as bilateral postcentral gyri and inferior parietal lobule more than the sighted group. The sighted subjects activated bilateral temporal cortices (STG, MTG) and bilateral occipital clusters (inferior occipital gyri) more than the blind subjects (Fig. 3A, Table 3).

For the reading specific contrast (words > non-linguistic control), the blind subjects activated bilateral occipital areas, including vOT and the left frontal cluster (IFG, precentral gyrus, Fig. 4, Table S3 in the Supplementary Materials). In the sighted subjects, we observed activation in the left vOT and left precentral and postcentral gyri. The blind subjects activated bilateral vOT, left calcarine and bilateral IFG more than the sighted subjects (Fig. 3, Table S3 in the Supplementary Materials). The inverse comparison showed that two right hemisphere clusters in occipital and temporal cortices were activated more by the sighted group. The region of common activation between the sighted and the blind was present in the left vOT. Individual peaks analysis in the left vOT cortex replicated Reich et al., (2011) results. The peaks from the sighted and the blind subjects were localized in very similar sites (see Supplementary Materials for more details).

When words reading was compared to pseudowords reading, the difference was revealed only in the sighted group. During pseudowords reading, the sighted subjects activated bilateral parietal clusters, left IFG and precentral gyrus and left occipital cluster more than during words reading (Figure S3, Table S4). Interestingly, the conjunction of the activations specific to pseudowords reading (pseudowords > non-linguistic control) between the sighted and the blind group included additional regions, in the left IFG extending to precentral gyrus, when compared to the words reading conjunction.

For speech processing, the blind subjects activated a much broader network than the sighted group (Fig. 2B, Table S5 in the Supplementary Materials). In the speech sensitive contrasts (words > baseline), the blind group, apart from the bilateral temporal activation present also in the sighed group, activated the occipital cortex with bilateral vOT and right IFG more than the sighted group (Fig. 3, Table 3). When speech specific (words > non-linguistic control) activations were analysed, the blind subjects activated the bilateral temporal regions and left vOT, whereas the sighted subjects activated only the temporal cortex (Fig. 4B, Table S6 in the Supplementary Materials). Thus, the left vOT cluster was activated more by the blind than by the sighted during speech-specific contrast (Fig. 3).

3.2. Speech-reading convergence

Conjunctions of the speech and reading sensitive activations examined in the blind and the sighted subjects revealed different regions of the speech-reading convergence in the two groups (Fig. 5, Table 4). In the blind group, conjunction revealed significant clusters in the bilateral vOT (extending to MTG in the left hemisphere). In the sighted subjects, the bilateral MTG/STG regions were the sites of convergence.

These results were confirmed by individual convergence analysis. Individual convergence was examined using two methods: counting significant voxels in the individual conjunction maps (Preston et al., 2016) and correlation of the reading and speech processing related contrast estimates (Rueckl et al., 2015) in specific ROIs (left MTG/STG, right STG, left vOT). We observed greater convergence, measured as the number of overlapping voxels, in the sighted subjects in the left MTG/STG ($U = 147.00$, $p_{corrected} = 0.004$). On the other hand, the blind subjects presented greater convergence in the left vOT ($U = 180.00$, $p_{corrected} = 0.02$). There was no difference between the groups in the right STG ($U = 226.00$, $p_{corrected} = 0.186$).

Table 2
Reading sensitive activations (words > baseline), H - hemisphere, x,y,z – cluster peak coordinates, t –value of the t-statistics from the peak, vox - number of voxels, *p* - cluster level *p*-value, FWE corrected structures spanning more than 50 voxels are reported in each cluster.

Brain region	H	x	y	z	t	vox	*p*
Blind							
Precentral Gyrus, Postcentral Gyrus, Inferior Parietal Lobule, Inferior Frontal Gyrus (p. opercularis, triangularis, orbitalis), Supramarginal Gyrus	L	-58	10	16	8.31	2961	< 0.001
Fusiform Gyrus, Cerebellum, Inferior Temporal Gyrus, Middle Temporal Gyrus, Inferior Occipital Gyrus, Middle Occipital Gyrus, Lingual Gyrus	L	-42	-68	-8	7.41	2017	< 0.001
Inferior Temporal Gyrus, Fusiform, Cerebellum, Middle Temporal Gyrus	R	50	-68	-2	6.06	795	0.001
Postcentral Gyrus, Precentral Gyrus, Inferior Frontal Gyrus (p. opercularis), Inferior Parietal Lobule, Supramarginal Gyrus, Superior Parietal Lobule	R	52	-2	50	5.87	1359	< 0.001
Sighted							
Middle Temporal Gyrus, Superior Temporal Gyrus, Inferior Occipital Gyrus, Middle Occipital Gyrus, Fusiform Gyrus, Inferior Temporal Gyrus, Cerebellum, Lingual Gyrus, Calcarine, Rolandic Operculum, Postcentral Gyrus Supramarginal Gyrus, Superior Occipital Gyrus, Heschl's Gyrus, Superior Temporal Pole, Insula	L	-28	-92	-4	18.12	5677	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Cerebellum, Inferior Temporal Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus, Middle Occipital Gyrus, Precentral Gyrus, Inferior Frontal Gyrus (p. opercluaris, triangularis), Calcarine, Middle Frontal Gyrus, Lingual Gyrus, Cuneus, Superior Occipital Gyrus, Rolandic Operculum, Superior Temporal Pole, Superior Frontal Gyrus, Supramarginal Gyrus, Postcentral Gyrus	R	22	-96	4	15.72	5173	< 0.001
Precentral Gyrus, Postcentral Gyrus	L	-50	0	50	5.75	502	< 0.001
Inferior Frontal Gyrus (p. triangularis, orbitalis)	L	-50	36	-6	4.74	270	0.008
Blind & Sighted (conjunction)							
Fusiform Gyrus, Inferior Temporal Gyrus, Inferior Occipital Gyrus, Middle Temporal Gyrus, Middle Occipital Gyrus, Cerebellum	L	-44	-70	-8	6.74	967	< 0.001
Inferior Temporal Gyrus, Cerebellum, Fusiform Gyrus, Middle Temporal Gyrus	R	42	-60	-8	5.59	530	0.002

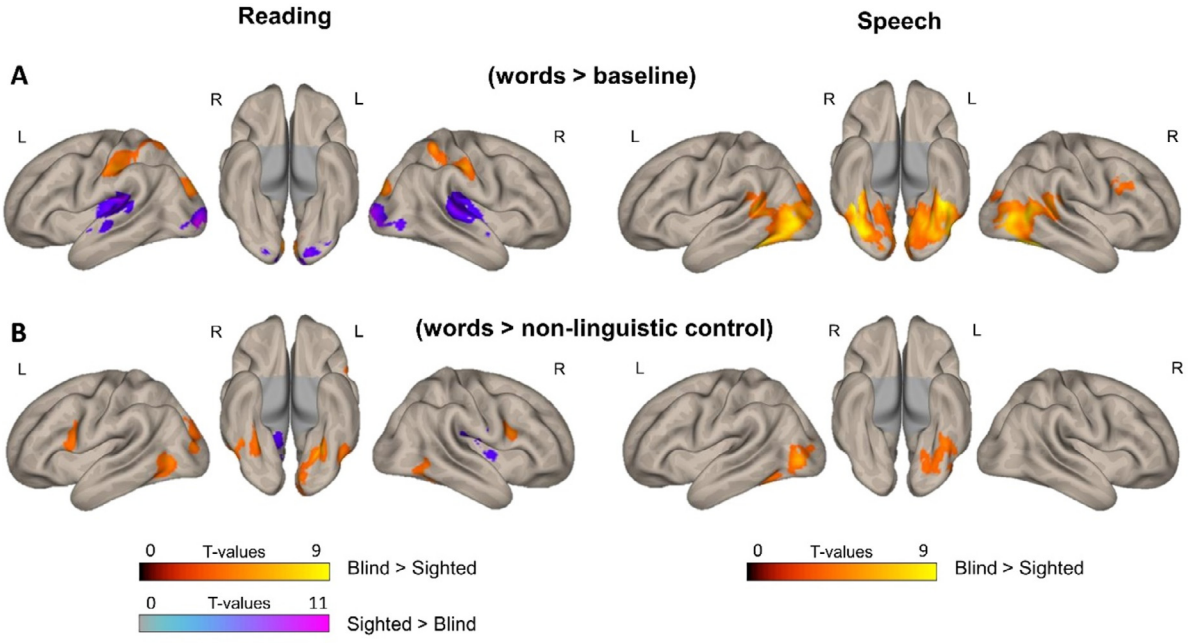

Fig. 3. Group differences for reading and speech A) sensitive (words > baseline) and B) specific (words > non- linguistic control) contrasts, L – left hemisphere, R – right hemisphere. All contrasts at voxelwise $p < 0.001$ and cluster wise $p < 0.05$ FWE corrected.

In the sighted group, the correlations between the reading and speech sensitive (words > baseline) contrast estimates were significant in all of the ROI (right STG: $r = 0.68$, $p_{corrected} < 0.001$; left MTG/STG: $r = 0.46$, $p_{corrected} = 0.020$; left vOT, $r = 0.67$, $p_{corrected} < 0.001$). In the blind group, however, the correlation was significant only in the left vOT ROI (right STG: $r = 0.007$, $p_{corrected} = 0.974$; left MTG/STG: $r = 0.31$, $p_{corrected} = 0.368$; left vOT, $r = 0.68$, $p_{corrected} < 0.001$). Interestingly, when we compared the correlation coefficients in the right STG, left MTG/STG and left vOT between the groups, the only significant difference was found in the right STG (Fisher's $Z = -2.74$, $p_{corrected} = 0.009$), with the sighted group presenting higher correlation than the blind. Differences between the other two coefficients were not significant (left MTG/STG: Fisher's $Z = -0.60$, $p_{corrected} = 0.548$; left vOT: Fisher's $Z = 0.08$, $p_{corrected} = 0.469$).

3.3. Speech-reading convergence in the left vOT in the blind

The left vOT turned out to be the main region of speech-reading convergence in the blind. To facilitate interpretation of this result and to examine the nature of speech-related activation in this region we con-

Table 3
Group differences in reading and speech sensitive contrasts, H - hemisphere, x,y,z – cluster peak coordinates, t – value of the t-statistics from the peak, vox - number of voxels, *p* - cluster level *p*-value, FWE corrected, structures spanning more than 50 voxels are reported in each cluster.

Brain region	H	x	y	z	t	vox	*p*
Reading sensitive contrasts (words > baseline)							
Blind > Sighted							
Cuneus, Calcarine, Superior Occipital Gyrus, Lingual Gyrus, Middle Occipital Gyrus, Cerebellum, Superior Parietal Lobule	L/R	0	-84	18	7.34	2043	< 0.001
Postcentral Gyrus, Inferior Parietal Lobule, Supramarginal Gyrus, Superior Parietal Lobule, Precentral Gyrus	R	48	-22	40	6.15	1066	< 0.001
Inferior Parietal Lobule, Postcentral Gyrus, Superior Parietal Lobule, Supramarginal Gyrus, Precuneus	L	-46	-28	36	5.90	1159	< 0.001
Sighted > Blind							
Inferior Occipital Gyrus, Middle Occipital Gyrus, Lingual Gyrus	L	-24	-94	-2	11.04	717	< 0.001
Inferior Occipital Gyrus, Middle Occipital Gyrus, Calcarine, Lingual Gyrus, Superior Occipital Gyrus	R	24	-98	6	8.36	672	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Insula, Rolandic Operculum, Heschl's Gyrus	L	-40	-34	18	7.42	1980	< 0.001
Superior Temporal Gyrus, Insula, Heschl's Gyrus, Rolandic Operculum	R	62	-28	10	6.40	1723	< 0.001
Speech sensitive contrasts (words > baseline)							
Blind > Sighted							
Lingual Gyrus, Calcarine, Middle Temporal Gyrus, Middle Occipital Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus, Cuneus, Superior Temporal Gyrus, Inferior Temporal Gyrus, Cerebellum, Superior Occipital Gyrus, Supramarginal Gyrus, Angular Gyrus	L/R	-38	-52	-14	9.35	13097	< 0.001
Inferior Frontal Gyrus (p. opercularis, triangularis)	R	48	20	30	4.59	216	0.048
Sighted > Blind							
No suprathreshold clusters							

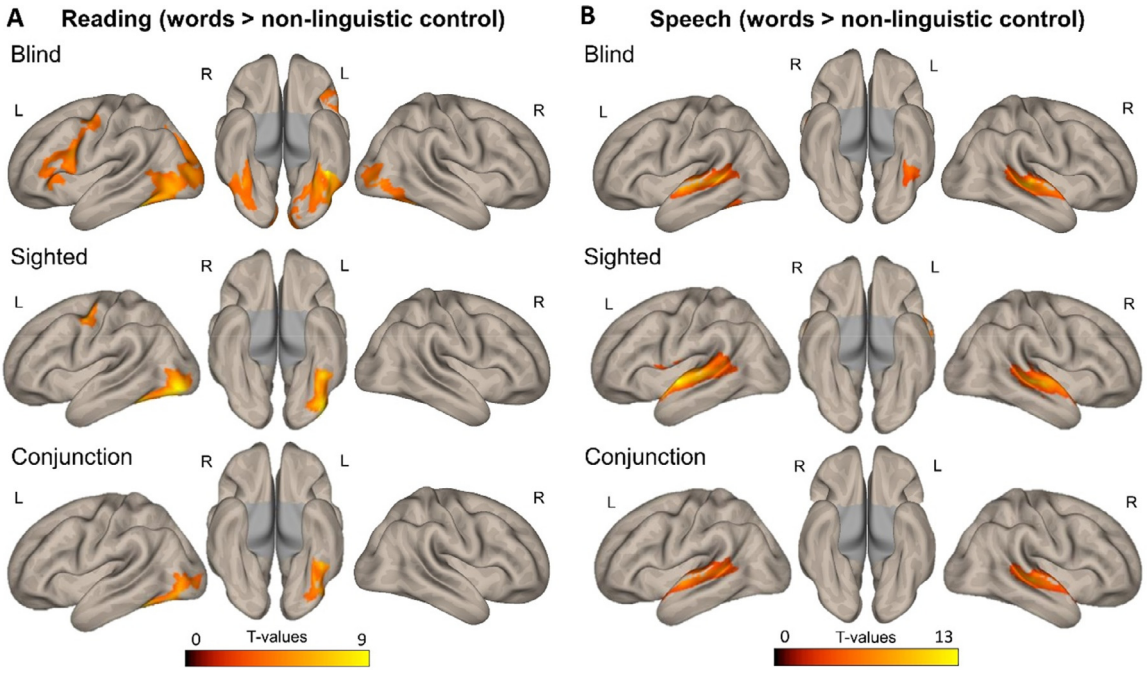

Fig. 4. A) Reading and B) speech specific (word > non-linguistic control) activations, L – left hemisphere, R – right hemisphere. All contrasts at voxelwise $p < 0.001$ and cluster wise $p < 0.05$ FWE corrected.

Table 4
Speech-reading convergence, H - hemisphere, x,y,z – cluster peak coordinates, t – value of the t-statistics from the peak, vox - number of voxels, *p* - cluster level *p*-value, FWE corrected, structures spanning more than 50 voxels are reported in each cluster.

Brain region	H	x	y	z	t	voxe	*p*
Blind							
Fusiform Gyrus, Inferior Temporal Gyrus, Cerebellum	R	38	-62	-20	5.82	431	0.013
Fusiform Gyrus, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Middle Temporal Gyrus, Middle Occipital Gyrus, Cerebellum	L	-44	-56	-12	5.63	1516	< 0.001
Sighted							
Superior Temporal Gyrus, Middle Temporal Gyrus	R	58	-26	0	5.12	496	< 0.001
Middle Temporal Gyrus, Superior Temporal Gyrus	L	-46	-38	22	4.89	677	< 0.001

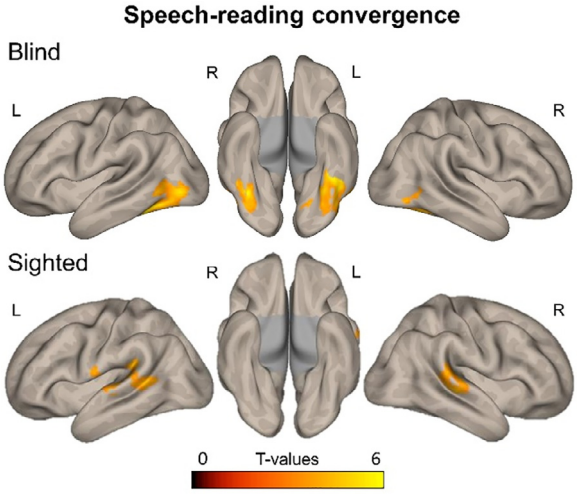

Fig. 5. Speech-reading convergence in blind and sighted participants, L – left hemisphere, R – right hemisphere. All contrasts at voxelwise $p < 0.001$ and cluster wise $p < 0.05$ FWE corrected.

ducted additional post-hoc analyses following Planton et al. (2019). We were interested to what extent reading and speech-processing related activations in the left vOT are separated.

First, we looked at the overlap between individual reading and speech specific (words > non-linguistic control) activation in the left vOT. Activation for reading contrast was more extensive – 321.46 voxels on average (SD = 287.76) than the activation for speech contrast – 138.00 voxels on average (SD = 145.45). One subject did not show significant activation for the reading contrast and ten failed to show activation for the speech contrast in the left vOT (no significant voxels in the volume of search at $p < 0.001$, uncorrected). Fifteen subjects that presented significant activation for both conditions were tested for the overlap. Out of the fifteen, two subjects did not show any overlap between the reading and speech specific activations. On average, 113.62 voxels (SD = 124.86) were common for the reading and speech processing related ROIs. The overlap constituted 25.39% (SD = 29.16%) of the area of reading specific activations on average and 69.08% (SD = 35.53%) of the area of speech specific activations.

Secondly, we wanted to test whether the voxels activated by reading are also active during speech processing. To this end, speech specific contrast estimates were extracted from the individual reading-related ROIs (for all, 25 blind subjects). The Wilcoxon signed-rank test showed that the reading specific regions were also active for speech specific contrasts ($Z = 271.00$, $p < 0.001$).

As the last post-hoc analysis, we wanted to test whether the left vOT in the blind, in contrast to the sighted, belongs to the modality independent language network. In the blind group the left vOT was active during reading as well as during speech processing, which may suggest its engagement in language processing in general, independently of the modality. We used seed-to-voxel task-related correlation analysis, as functional connectivity is considered to be a measure of network integration (Friston, 2011) and we compared connectivity during reading and speech processing in both groups.

The regions that exhibited significant correlation with the left vOT activity in the blind did not differ between the reading and speech processing conditions, except one cluster in right superior frontal gyrus (Table S7 in the Supplementary Materials). In the blind group, the left vOT proved to be connected with broad language network (bilateral MTG/STG, inferior frontal and precentral/postcentral gyri), as well as with the occipital cortex (V1/V2 loci, see Figure S3 and Table S7 in the Supplementary Materials) during reading and speech processing. In the sighted subjects, the activity of the left vOT was correlated with occipital cortex activity, as well as regions in the parietal (inferior parietal lobule) and frontal cortex (IFG, precentral/postcentral gyri, see Figure S3 and Table S8 in the Supplementary Materials) during both reading and speech processing.

When compared to the sighted subjects, the blind subjects showed greater correlation during reading between the left vOT and the occipital cortex (V1/V2) (Fig. 6, Table S9 in the Supplementary Materials). During speech processing, the left vOT activity in the blind subjects correlated with left perisylvian areas (left MTG/STG, left IFG) more than in the sighted subjects. The functional connectivity results suggest that in the blind, the left vOT belongs to a broad, modality independent language processing network, but it is not the case in the sighted.

4. Discussion

This study aimed to test the limits of the universality of the neural reading network by comparing visual and Braille reading between the sighted and the early blind populations. To our knowledge, this is the first report of speech-reading convergence in the blind population directly compared to such convergence in the sighted population. The only study previously looking at the phonetic processing of Braille and spoken meaningless syllables in the blind reported convergence in the right precentral gyrus and the cerebellum and did not include sighted control group (Pishnamazi et al., 2016). Contrary to our hypothesis, speech-reading convergence was found to be present in the blind in different regions than in the sighted subjects. We think that the discrepancy between the regions of speech-reading convergence in the blind and in the sighted reflects the differences between visual and Braille reading networks (disengagement of the MTG/STG region in the blind), as well as the alterations in the speech processing network in the visually deprived population (engagement of the left vOT in speech processing).

4.1. Similarities and differences between visual and Braille reading network

As expected, the blind subjects engaged the visual cortex while reading Braille to a larger extent and probably in a different way than the

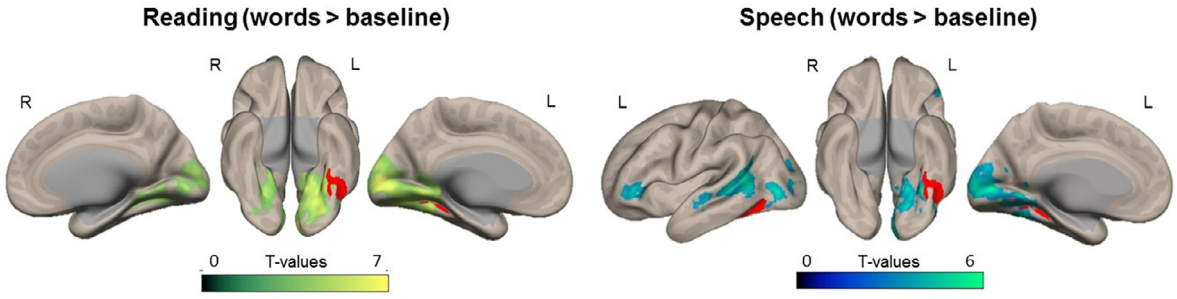

Fig. 6. Regions with higher functional connectivity with the left vOT region (seed, marked in red) during A) reading and B) speech processing in the blind group than in the sighted group, L – left hemisphere, R – right hemisphere. All contrasts at voxelwise $p < 0.001$ and cluster wise $p < 0.05$ FWE corrected.

sighted subjects. In the blind, activation in the occipital cortex was reading specific (Fig. 4A), whereas in the sighted subjects only reading sensitive (Fig. 2A). It was located in the V1/V2 sites, consistent with previous findings (Sadato et al., 1998, Burton et al., 2002, Gizewski et al., 2003) that suggest occipital cortex engagement in high order language processing in the blind instead of the low level sensory processing in the sighted. Unexpectedly, in the reading sensitive contrast (words > baseline), the sighted subjects activated the temporal regions (MTG/STG) more than the blind (Fig. 3A). Temporal activations were observed in the blind subjects only during spoken words processing but were not active during reading (Fig 2 and Fig. 4). In the sighted population, MTG/STG region is involved in phonological and semantic processing (Price, 2012, Glezer et al., 2016) and multimodal integration of linguistic stimuli (Hickok & Poeppel, 2007). The temporal cortex was also shown to be involved in phonological and semantic processing of spoken stimuli in the blind (Burton et al., 2003, Arnaud et al., 2013). The phonological processing during Braille reading was never directly tested. However, studies looking at single Braille words reading usually fail to report extensive temporal activations similar to these observed in the sighted (Burton et al., 2002; Gizewski et al., 2003; Kim et al., 2017). The disengagement of the MTG/STG region in the blind may imply that this region fails to be co-opted to reading in the blind population. The functions fulfilled by the temporal cortex in the sighted during reading may be, at least to some extent, taken over by other regions, possibly residing in the occipital cortex.

The differences between the activations of the blind and the sighted group during reading may potentially be related to different modality used for reading. Nevertheless, we think that it is unlikely, as it was shown (Siuda-Krzywicka et al., 2016) that sighted subjects (without visual deprivation) trained in tactile Braille reading exhibited activation in classical reading network, including persylvian regions, when reading Braille. The changed modality of reading did not change the language sensitive network.

We have also observed changes to the speech processing network in the blind group. The blind subjects activated occipital regions, including the left vOT to a larger extent than the sighted subjects in the speech-specific contrast (words > non-linguistic control, see Fig. 3). Sensitivity to speech in the left vOT in the blind had already been reported in the literature (Bedny et al., 2011, Burton et al., 2003, Noppeney, 2003, Röder et al., 2002) and it was shown that this region was sensitive to syntactic complexity of spoken sentences (Lane et al., 2015, Kim et al., 2017). Our results extend these findings, showing that the left vOT is sensitive also to single spoken words perception (see also Kim et al., 2017) and that activation in this region largely (albeit not completely) overlaps with the reading-related activation. Given no differences in the functional connectivity of the left vOT region between the reading and speech processing condition and strong connections with the language-related regions during speech processing (for similar results in resting state paradigm see Liu et al., 2007, Abboud & Cohen, 2019), we conclude that the left vOT belongs to modality independent language network in the blind.

Our study replicates the findings of Reich and colleagues (2011) showing that the common region between the visual and the Braille reading network is the left vOT. The results of the analysis of the individual peak showed that Braille reading-related peaks did not differ from the visual reading-related peaks in any of the peak coordinates. Additionally, the clustering analysis did not divide the peaks into clusters that would closely correspond to the two groups. The two clusters included peaks from both blind and sighted groups.

The additional analysis of pseudowords reading indicated that Braille word reading activates more regions in common with visual pseudowords reading (left IFG and precentral gyrus together with left vOT) than with visual word reading (Fig. S3, Table S4 in Supplementary Material). While these structures were more active for visual pseudoword than word reading, we did not observe any differences between Braille pseudoword and word reading. Behavioural studies suggest that Braille reading is more sequential (sublexical route employed instead of orthographic route) than visual reading (Veispak et al., 2012). Our results are in line with these findings and imply intensified involvement of the articulatory processes, independent of the lexical status and frequency of the perceived stimuli (Hickok and Poeppel, 2007).

4.2. Speech-reading convergence

Since we have observed changes to both reading and speech processing networks between the blind and the sighted, the regions of the speech-reading convergence also turned out to be different. The main regions of convergence in the blind group were bilateral vOT and there was no overlap present in the temporal sites (Fig. 5), contrary to what was observed in the sighted subjects (Rueckl et al., 2015). This was confirmed by individual overlap analyses with more voxels common for speech processing and reading in the sighted than in the blind in the left MTG/STG and a reversed pattern for the left vOT. In the blind subjects, left vOT regions sensitive to reading were also significantly active for speech processing in more than 50% of our sample.

Our results of the speech-reading convergence were based on the language-sensitive contrasts. Observed activations may have included areas not only involved in language processing but also in multisensory processing (e.g. STS, Beauchamp et al., 2008). Nevertheless, we think that the results of the speech-reading convergence are language-specific, at least in the blind group. When we looked at the convergence of the language-specific contrasts (words > non-linguistic control, contrary to previous studies using contrasts comparing the language task to baseline) the left vOT cluster was still significant at the trend level ($p_{cluster} = 0.061$, Table S10, Figure S5) in the blind group. In the sighted group this conjunction did not yield any significant results.

We cannot exclude that the convergence observed in the sighted group in the perisylvian areas might represent a mixture of language and multisensory processing. This may also be the case of the previous studies (Chyl et al., 2018; Marks et al., 2019; Preston et al., 2016; Rueckl et al., 2015) since all of them compared the experimental task to baseline only. On the other hand, the evidence coming from children's studies argues that speech-reading convergence does not merely reflect sensory inputs (multisensory processing), as it appears only after reading acquisition (Chyl et al. 2018) and is relevant for the behavioural reading outcomes (Preston et al. 2016, Marks et al. 2019). Additionally, studies reported language-specific activation in the perisylvian regions. One example of such a study is Malins et al. (2016) paper where participants were presented with stimuli very similar to the ones employed in the current study but instead of passive perception, they were asked to memorize them. It is possible that if we employed a more engaging linguistic task for the participants, we would have observed speech-reading specific conjunction in the perisylvian areas.

The supposed mechanism of the speech-reading convergence is that the regions that analyse spoken language before literacy acquisition become co-opted for written language processing (Liberman, 1992). In the blind the main region of speech-reading convergence is the left vOT. Following Liberman's logic, it would mean that the left vOT is processing speech before reading acquisition, becomes co-opted for Braille reading afterwards, which results in the observed speech-reading convergence. Although suggestions of the early sensitivity of the vOT to speech have been made based on a study with literate blind children as participants (Bedny et al., 2015), so far there has been no evidence of such sensitivity in the preliterate or illiterate blind subjects.

The left vOT was repeatedly shown to be active during Braille reading (Büchel, Price, and Friston, 1998, Sadato et al., 1998) displaying evidence for orthographic repetition suppression (Rączy et al., 2019) similar to that observed in the sighted population (Glezer et al., 2016). This was considered a proof for selective specialization for written language processing and an argument for assigning the role of orthographic representation storage to this region. Nevertheless, Planton and col-

leagues (2019) demonstrated that left vOT cortex of the sighted subjects responds to spoken sentences, in a task that does not demand any access to orthographic representations (cf. Dehaene and Cohen, 2011). Additionally, a recent TMS study suggested that the vOT holds segregated neural populations selectively responding to visually and aurally presented language (Pattamadilok et al., 2019). Pattamadilok and colleagues (2019) put forward a hypothesis that the sensitivity of the left vOT is connected to reading acquisition, as during this process spoken language is repeatedly associated with written language. A similar mechanism could be present in the blind and could be reinforced by cognitive and behavioural characteristics of Braille reading, such as the more extensive use of the sublexical route and recurrent involvement of articulatory processes. This could lead to both reading and speech sensitivity in the left vOT.

Our results support such a hypothesis. Although on the group level, the left vOT was sensitive also to spoken words processing, this activity could be observed in only some of the blind participants. Moreover, the analysis of the overlap between reading and speech processing related activations in the left vOT, has shown that the overlap is not perfect, which means that some parts of this region may be specialized in processing of the language stimuli only from one modality. As the MTG/STG areas are disengaged during Braille reading (Fig. 2 and Fig. 4), we hypothesize that the vOT becomes specialized also in phonological processing in the visually deprived population. It would be in line with the report of Arnaud and colleagues (2013) on the repetition suppression effect in the left vOT during the presentation of spoken vowels in the blind. As suggested by Pattamadilok and colleagues (2019), and consistently with our results, processing of spoken and written language could be conducted by segregated neural populations.

4.3. Limitations

The current study had some important limitations. Firstly, we used a passive task and thus we were not able to control if subjects paid attention to all of the stimuli. Secondly, the task may have been more engaging for the blind subjects than for the sighted subjects. Braille reading is more sequential and slower, it also requires managing additional device – the Braille displayer instead of simply looking at the screen. This may be the reason why we observed in general more extensive activation in the blind group than in the sighted group. The stimuli used in the experiment were high frequency, short words that are very easily and automatically read by sighted subjects. Inclusion of an additional linguistic task could make it more comparable between the sighted and the blind populations. Additionally, a more complex linguistic task during speech processing could help to uncover the specific role of the left vOT in the blind language network.

5. Conclusions

Our results indicate that the universality of the reading network across modalities is limited. What appears to be more universal, is the coupling of speech processing and reading on the neuronal level, since speech-reading convergence is also present in the blind population. We have shown that both visual and Braille reading engage the left vOT region but only in the blind, this region belongs to a modality independent language network. In addition, significant similarities between visual pseudoword reading and Braille word reading on the neural level confirm increased seriality and lower automatization of Braille reading. Despite these compelling analogies, plastic changes following visual deprivation are evident. Disengagement of the bilateral MTG/STG during Braille reading combined with increased sensitivity of the left vOT to speech processing may suggest differences in the phonology processing network in visually deprived populations.

Declaration of Competing Interest

The authors declare no competing interests.

Credit authorship contribution statement

Gabriela Dzięgiel-Fivet: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Visualization, Writing - original draft, Writing - review & editing. **Joanna Plewko:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing - review & editing. **Marcin Szczerbiński:** Conceptualization, Data curation, Resources, Writing - review & editing. **Artur Marchewka:** Conceptualization, Resources, Writing - review & editing. **Marcin Szwed:** Conceptualization, Resources, Writing - review & editing. **Katarzyna Jednoróg:** Conceptualization, Data curation, Funding acquisition, Project administration, Methodology, Supervision, Writing - review & editing.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.117851.

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