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The influence of visual deprivation on the neural network for language

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Table of contents

Abstract

The functional organisation of the human brain is influenced both by innate mechanisms and individual experience. Spoken language processing, an evolutionary old skill, occurs in a neural network universal for different languages. On the other hand, reading is a skill that appeared in human evolution quite late and thus is an excellent example of neural plasticity connected to learning a new skill. Additionally, reading can be performed using not only vision but also touch. Braille alphabet is a script used by the blind population for reading using the sense of touch. Blindness enables us to see which aspects of the neuronal organisation are fixed and which change with altered experience.

The current thesis focuses on the plastic changes in the organisation of the neural language network following visual deprivation. Three studies were conducted. The first focused on mapping the spoken and reading neural networks in the blind population and comparing them to the organisation of language processing in the sighted. Speech-reading convergence – a phenomenon thought to be universal in print reading was also tested for the first time in the blind population. The results of Study 1 revealed that speech-reading convergence was present in the blind subjects, but in different areas. It was found in the ventral occipitotemporal cortex (vOT), instead of the perisylvian regions. In the blind group, the vOT was active not only during reading, as in the sighted, but also during speech processing. The temporal cortex, which is involved in phonological processing in the sighted population, was disengaged during Braille reading.

Thus, in Study 2, the vOT engagement in phonological processing was studied in the blind and the sighted. The blind subjects activated the left vOT during auditory phonological processing to a larger extent than the sighted subjects. However, this activation seemed not to be phonology specific. In the blind, the left vOT presented a similar activation during linguistic processing as other regions of the language network. The results of the second experiment suggest that the vOT plays a more general role in language processing in the blind population due to changed input to this structure arising from visual deprivation.

Study 3 tested the differences in the cognitive correlates of print and Braille reading. Additionally, the relationship between literacy-related skills and age was studied using a cross-sectional design. The results of the third experiment indicate that the change in the modality used for reading introduces some alterations to the cognitive mechanisms of reading. Limits of the tactile modality - lower processing speed and the sequential nature of the processing augment the importance of the haptic factors for Braille reading and may cause minor deficits in some domains. On the other hand, different demands induced by the changed modality strengthen phonological skills and short-term memory. Yet, the developmental trajectory of literacy skills remains unchanged in the blind, as there were no differences in the correlations with age between the groups.

Research presented in the thesis demonstrates that visual deprivation influences the functional organisation of both evolutionary old (spoken language) and newly learned skills (reading) on the neural and behavioural levels. Results underline the importance of individual experience for the organisation of specialised neural networks and are in line with the pluripotent cortex hypothesis of neural plasticity.

Streszczenie

Na funkcjonalną organizację ludzkiego mózgu wpływ mają zarówno wrodzone mechanizmy rozwojowe, jak i indywidualne doświadczenie. Przetwarzanie języka mówionego, umiejętność, która w toku ewolucji gatunku ludzkiego pojawiła się dość wcześnie, angażuje sieć neuronalną, która jest uniwersalna dla użytkowników bardzo zróżnicowanych języków. Język można przetwarzać także w formie pisanej. Czytanie jest zdolnością poznawczą stosunkowo nową w ludzkiej filogenezie, pozwala więc na obserwację neuronalnej plastyczności związanej z nabywaniem nowych umiejętności. Ponadto, czytanie jest możliwe nie tylko z wykorzystaniem zmysłu wzroku, lecz także za pomocą dotyku. Alfabet Braille'a jest systemem pisma używanym przez osoby niewidome do czytania dotykowego. Badanie osób niewidomych umożliwia sprawdzenie, które aspekty organizacji funkcjonalnej mózgu są stałe, a które ulegają zmianom pod wpływem indywidualnego doświadczenia. Niniejsza praca skupia się na plastycznych zmianach w organizacji mózgowej sieci przetwarzającej język wywołanych utratą wzroku. Przeprowadzono trzy badania. Pierwsze miało na celu zbadanie organizacji sieci językowej przetwarzającej mowę i pismo u osób niewidomych oraz porównanie jej do organizacji sieci językowej u osób widzących. Pokrywanie się sieci przetwarzającej język mówiony oraz pisany - zjawisko uważane za uniwersalne dla czytania wzrokowego, zostało po raz pierwszy zbadane w populacji niewidomej. Wykazano, że pokrywanie się sieci związanej z językiem mówionym i pisanym można zaobserwować również u osób niewidomych, jednak w innych obszarach niż u osób widzących. Pokazano, że to brzuszna kora potyliczno-skroniowa jest miejscem przetwarzającym zarówno mowę, jak i pismo u osób niewidomych, zamiast obszarów perisylwialnych, w których obserwuje się to zjawisko u osób widzących. Obszary skroniowe, które u osób widzących wiązane są z przetwarzaniem fonologicznym, nie były zaangażowane w równym stopniu w czytanie brajlem, co w czytanie wzrokowe.

W związku z tym, drugie badanie skupiło się na analizie zaangażowania brzusznej kory potyliczno-skroniowej w przetwarzanie fonologiczne bodźców słuchowych u osób niewidomych i widzących. Mimo iż, stwierdzono większe zaangażowanie tej struktury w przetwarzanie fonologiczne u osób niewidomych niż widzących, aktywacja nie okazała się być specyficznie związana z przetwarzaniem fonologicznym. U osób niewidomych, lewa brzuszna kora potyliczno-skroniowa aktywowana była w czasie przetwarzania językowego w sposób podobny do innych obszarów, klasycznie zaliczanych do sieci językowej. Wyniki drugiego badania sugerują, że u osób niewidomych brzuszna kora potyliczno-skroniowa pełni w przetwarzaniu językowym rolę mniej specyficznie związaną z czytaniem niż u osób widzących. Może to być związane ze zmianą natury informacji sensorycznej, która dociera do tego obszaru wskutek wczesnej utraty wzroku.

Badanie trzecie analizowało różnice w poznawczych korelatach czytania wzrokowego i dotykowego. Dodatkowo, związek umiejętności istotnych dla czytania z wiekiem został zbadany w schemacie badania poprzecznego. Wyniki badania trzeciego wskazują, że zmiana zmysłu używanego do czytania wprowadza pewne zmiany do poznawczych mechanizmów związanych z tym procesem. Ograniczenia związane z wolniejszym tempem oraz sekwencyjną naturą przetwarzania dotykowego podnoszą

znaczenie czynników dotykowych dla czytania brajlem, a także mogą powodować nieznaczne deficyty w innych obszarach. Z drugiej strony, zmiana modalności zmienia wymagania nakładane na system poznawczy przetwarzający pismo, co może prowadzić do podniesienia poziomu umiejętności fonologicznych oraz wzmocnienia pamięci krótkotrwałej. Nie znaleziono różnic międzygrupowych w korelacjach między umiejętnościami związanymi z czytaniem a wiekiem, co sugeruje, że trajektoria rozwoju tych umiejętności pozostaje niezmieniona u osób niewidomych.

Badania przedstawione w niniejszej pracy pokazują, że wczesna utrata wzroku wpływa zarówno na organizację funkcjonalnej sieci mózgowej, jak i behawioralną charakterystykę umiejętności filogenetycznie starych (przetwarzanie mowy) oraz nowych (czytanie). Wyniki opisane w rozprawie podkreślają znaczenie indywidualnego doświadczenia na organizację wyspecjalizowanych sieci neuronalnych i są zgodne z hipotezą o wielopotencjalności kory, dotyczącą między-zmysłowej plastyczności mózgu.

State of the Art

Language as a cognitive skill and its functional organisation in the brain

Language is a cognitive skill that has become the main tool of communication in humans (Kurcz, 2001). It is a complex ability, based on describing the world and its elements using symbolic names but also dependent on high-level operations enabling the formulation of abstract ideas. As a cognitive process, it involves both domain-general mechanisms that are shared by many cognitive skills, and domain-specific operations, unique for language (Hagoort, 2019). Domain-general mechanisms include the integration of the perceived spoken utterance into the context of an exchange or control over word choice in a given social situation. The domain-specific elements of the linguistic process are for example retrieval of word meaning or its phonological form. This thesis will focus more on domain-specific linguistic processes.

These processes are considered to be connected to the activity of temporal and frontal regions around the Sylvian fissure. Reports on left-lateralized regions being hubs of language production and perception laid the foundation for modern neuroscience (Broca, 1861; Wernicke, 1874). However, it is now evident that both hemispheres are activated by linguistic tasks and probably process different aspects of linguistic experience (Lindell, 2006). Traditional models of the language network separated regions connected with language comprehension, placed in the temporal lobe (the Wernicke's area), from the ones engaged in language production residing in the inferior frontal cortex (Broca's area). The advances brought to the field by non-invasive imaging methods like positrion emission tomography (PET) and functional magnetic resonance imaging (fMRI) have shown that this model was oversimplistic. Different linguistic functions and characteristics of different time scales of speech perception overlap in many brain regions and can be separated only partially (Hamilton et al., 2021; Price, 2012).

One prominent model of language organisation in the brain is the dual stream model proposed by Hicock and Poeppel (2007). The authors postulated that spoken language is processed within the dorsal and ventral streams. The ventral stream is located in the bilateral superior and middle temporal cortices. It is thought to be responsible for mapping the acoustic signal onto meaning (speech recognition). The left and right hemisphere regions probably differ in their computational characteristics. The left hemisphere seems to be adapted more to analysing stimuli characterised by the high frequency of appearance in the speech stream (phonemic rate) but also to be less sensitive to the time resolution of the linguistic input. Right hemisphere regions are probably more engaged in the analyses of the lower frequency stimuli which may support their engagement in prosody processing. The dorsal stream of speech processing is considered more left-lateralized and located in the dorsal temporal lobe, posterior inferior frontal cortex and parietal operculum. These areas are thought to be engaged mainly in mapping the auditory input onto the articulatory networks, and thus in the control over speech production and phonological short-term memory.

Another division in the language network can be delineated between phonological and semantic processing. Phonological processing consists of perception, analysis and production of speech sounds, whereas semantic processing operates on word meanings and conceptual knowledge (Poldrack et al., 1999). A recent meta-analysis brought attention to the fact that both processes consist of representational and control elements (Hodgson et al., 2021). The phonological and semantic networks overlap in the middle and superior temporal cortices. Bilateral superior temporal cortices are thought to store phonological representations. Semantic representations seem more distributed, not only over the bilateral anterior temporal lobes but also in the inferior parietal cortex. The control over the phonological processing is connected to pars opercularis of the inferior frontal cortex, as well as the inferior parietal lobule. Semantic processes appear to be controlled by the bilateral inferior frontal cortex, left precentral gyrus, left posterior temporal cortex (both middle and inferior temporal gyri) and bilateral dorsomedial prefrontal cortex.

Though human language is far more complex than other animal systems of communication it must have appeared in the human cognitive repertoire through evolution probably early on in the history of our species (Pinker, 2003). Thus, humans are equipped with some linguistic capacity already at birth (e.g. precursors of social skills important for language acquisition - DeCasper, A. J., Fifer, W. P., Oates, J., & Sheldon, 1980; Fantz, 1963; Meltzoff & Moore, 1983, ability to produce vocalisations - Oller & Eilers, 1988, preference for native language over foreign language - Mehler et al., 1988). The human brain also seems to be organised in a way adapted to processing language early on. Perisylvian activations in response to speech, similar to patterns observed in adults, were shown in infants as young as three months (Dehaene-Lambertz et al., 2002, 2006; Imada et al., 2006). Linguistic capacity, as well as the functional organisation of the human brain to process language, are subject to development that can be influenced by environmental factors. Lack of contact with language in an early sensitive period can impede the acquisition of language (Curtiss, 1977; Mayberry, 2007) and early brain injury changes the organisation of the neural language network (Staudt, 2010). However, in typical conditions, the neural correlates of language are very similar between speakers of different languages (Malik-Moraleda et al., 2022; Rueckl et al., 2015).

Reading - translating spoken language into written language

Linguistic information can be encoded not only in the auditory form (speech) but also with the use of scripts. Reading is a cognitive skill that appeared in human cultural development not so long ago (Coulmas, 1996), and until recently was not evenly distributed in societies (Roser & Ortiz-Ospina, 2016). Thus, it can be viewed as an example of plasticity induced by environmental change and learning. It is unlikely that any brain region or neural system evolved in the biological sense to process written language. The oldest artefacts proving the existence of early writing systems are dated to be only 5400 years old (Dehaene, 2009), whereas the evolution of *Homo sapiens* from the first representants of the *Homo* genus took more than 2.5 million years (Knoll & Nowak, 2017). Most likely, existing neural networks, as well as more basic cognitive skills must be used to make reading possible (Dehaene & Cohen, 2007). Reading is a process of encoding linguistic meaning from arbitral symbols that need to be explicitly learned. Skills that show the strongest associations with reading development and efficiency are phonological awareness, and rapid naming, however, perceptual factors and working memory also play a role.

Phonological awareness (PA) is the capacity to understand the sound structure of words and the ability to manipulate this structure (e.g. count syllables, identify rhymes, or remove phonemes). Individual differences in PA correlate with individual differences in reading skills (Melby-Lervåg et al., 2012; Swanson et al., 2003). It is widely agreed that this relationship reflects reciprocal causation: while some PA skills facilitate literacy acquisition, others emerge (or get strengthened) as the result of explicit engagement with phonology and orthography that is inherent in learning to read and spell (Hulme et al., 2005; Powell & Atkinson, 2021; Rayner et al., 2001). The strength PA-reading relationship is moderated by several factors, such as writing system type (what level of representation is relevant for the system eg. syllables, morphemes, phonemes), or orthographic transparency (the consistency of mapping speech sounds into symbols). Significant correlations between PA and reading have been reported across all writing systems and all languages studied so far (Landerl et al., 2022). Those correlations tend to be stronger for alphabetic orthographies than the non-alphabetic ones (at least Chinese: Song et al., 2016). This is to be expected as the PA skills are probably less relevant when the writing system represents phonology very opaquely, and non-phonological cues have to be relied on heavily in order to recognize words. Among alphabetic orthographies, concurrent PA-reading correlations tend to be stronger when the orthography is more opaque (e.g. English) than when it is more transparent (e.g. German, Landerl et al., 2022). They also tend to be stronger for reading accuracy than fluency (Powell & Atkinson, 2021). These patterns seem consistent with the view that PA skills are most relevant when children go through the alphabetic/phonetic cue phase of learning to read, where the main challenge is learning to decode words accurately — the phase which lasts longer in more opaque alphabetic orthographies (Seymour et al., 2003). However, such conceptualization of the role of PA would also predict that PA – reading correlations should decrease with age and grade, which is not the case (Swanson et al., 2003) – they continue to be observed even in adult, proficient readers (Bell & Perfetti, 1994; Pratt & Brady, 1988; Warmington et al., 2013). It would also predict that, at any given grade level, PA-reading correlations would be stronger for poor readers than for average or good readers – yet the opposite is the case (Dębska et al., 2021; Swanson et al., 2003).

Rapid Automatized Naming (RAN) is the speed of naming highly familiar stimuli, such as colour patches, and line drawings of common objects, letters or digits. A large number of studies demonstrated that RAN is a robust correlate of reading skills (Araújo et al., 2015; Hjetland et al., 2017; McWeeny et al., 2022; Swanson et al., 2003). The RAN-reading relationship is robust across different writing systems and orthographies (Caravolas et al., 2012, 2019; Landerl et al., 2019; Moll et al., 2014; Ziegler et al., 2010) with only slight differences in the strength of the relationship. Namely, a stronger relationship was observed for non-alphabetic writing systems than the alphabetic ones (Araújo et al., 2015; Song et al., 2016) and - within alphabetic systems - stronger for opaque alphabetic orthographies than the transparent ones (Araújo et al., 2015). The correlational patterns summarised above are hard to account for by any univariate theory of what RAN actually measures. It is likely that belaying their apparent simplicity, RAN is an index of several cognitive processes that may be involved in successful literacy acquisition, such as the efficiency of phonological retrieval from long-term memory (Wagner et al., 1993; Wagner & Torgesen, 1987), precise cross-modal temporal integration that underpins orthographic learning (Wolf et al., 2000; Wolf & Bowers, 1999) or general speed of information processing (Kail et al., 1999; Kail & Hall, 1994), to name but some.

What makes RAN a particularly important predictor of reading is its relative independence from several other predictors, most notably PA (for a review, see Kirby et al., 2010; Norton & Wolf, 2012 for recent examples, see e.g. Caravolas et al., 2019; Dębska et al., 2021; Landerl et al., 2019). The connection between RAN and reading seems to be important throughout all stages of reading development and independently of age, at least as far as reading fluency is concerned (Dębska et al., 2021; Warmington et al., 2013).

Apart from PA and RAN other cognitive skills were also considered as potential cognitive correlates of reading. Learning to read poses demands on perceptual and memory systems and deficits in these domains have been hypothesised to impair the reading process (Swanson et al., 2009; Vidyasagar & Pammer, 2010). However, these skills do not explain a substantial proportion of variance when included in reading skills prediction models (Dębska et al., 2021; Hjetland et al., 2017) and are often disregarded in studies on reading correlates (Caravolas et al., 2013).

All writing systems map directly onto the spoken language. However, scripts differ in the way they encode spoken language. As mentioned above, differences in the writing systems (e.g. orthographic transparency) might to some extent affect the relationship between reading and its cognitive correlates, however, these differences are quite subtle.

Many similarities between the users of varying scripts are also observed on the neural level. Neural network activated during reading comprise occipital areas, inferior frontal gyrus (IFG) extending to precentral gyrus and supplementary motor areas (SMA), temporal areas of middle temporal gyrus (MTG), superior temporal gyrus (STG) and inferior parietal cortex, as well as ventral occipitotemporal (vOT) regions including inferior temporal gyrus (ITG) and fusiform gyrus (FG) (Martin et al., 2015). Rueckl et al. (2015) have shown that this network is activated independently of the script used for reading in four very different writing systems (from transparent alphabetic Spanish to opaque morpho-syllabic Chinese). Similar findings were reported in a meta-analysis based on several European languages by Martin et al. 2015, and by a recent study on early readers of Polish and English, thus very diverse orthographies (Chyl, Kossowski, et al., 2021). Moreover, Rueckl et al. study has also shown that the universally activated reading network overlaps largely with the regions activated for speech perception in all four languages.

This finding is very interesting in the context of the developmental studies of reading acquisition. During reading acquisition, the emergence of the convergence between reading and speech processing related activations was observed. In a Chyl et al. (2018) study on Polish children such overlap was present only in readers contrasting to the group of age-matched pre-readers. What is more, Preston et al. (2016) have shown that such an overlap predicts the reading efficiency of American early readers 2 years later. Additionally, the emergence of such overlap was dependent on the oral linguistic capacities of English-speaking children (Marks et al., 2019). These results may explain the astonishing universality of the neural correlates of reading between different scripts. The writing systems encode spoken language and thus the reading neural network may develop by encompassing the language network (Liberman, 1992). One region that does not conform to the speech-reading convergence principle but is definitely considered a part of the reading neural network in the ventral occipitotemporal cortex. The vOT, predominantly in the left hemisphere, is systematically activated during reading by readers of different scripts and levels of proficiency. The exact role of this region is debated. The left vOT region is considered either the storage of orthographic representations of letters, sublexical structures (bigrams or trigrams) and words (Dehaene & Cohen, 2011) or a site of integrative processes that combine bottom-up visual information with top-down predictions from language areas (Price & Devlin, 2011). What is certain is that the sensitivity to written words in this region emerges (Brem et al., 2014; Dehaene et al., 2015) and changes in the course of reading acquisition (Dehaene-Lambertz et al., 2018) in both school aged children and ex-illiterate adults. The connectivity of the vOT with language processing areas which already exists in young pre-readers probably has a shaping role in this development (Saygin et al., 2016).

The development of the written language-sensitive area in the vOT may be explained using the neuronal recycling hypothesis (Dehaene & Cohen, 2007). This theory states that evolutionary novel, cultural inventions such as reading localise on the pre-existing neural systems. The cultural inventions should settle in regions that are close enough to the given function and at the same time sufficiently plastic to acquire a new role. Anatomical and connectional constraints present in the human brain early on would limit the inter-cultural variation of the neural correlates of cultural inventions such as reading. The left vOT thus becomes the region specifically activated during reading thanks to its proximity to the visual cortex, early sensitivity to visual objects and connectivity with the spoken language areas.

As a result of reading acquisition, the left vOT becomes sensitive to language. This sensitivity may generalise over the linguistic input other than its written forms. Some activation of the left vOT was observed during speech processing (Ludersdorfer et al., 2016; Planton et al., 2019; Yoncheva et al., 2010). It was often explained as automatic activation of the orthographic codes stored in the left vOT (Dehaene et al., 2015). As such the activation of the vOT during speech processing is considered secondary to successful reading acquisition (Dehaene et al., 2010; Pattamadilok et al., 2017; Planton et al., 2019). Thus it is less pronounced in illiterates (Dehaene et al., 2010) or poor readers (Blau et al., 2010; Dębska et al., 2019; Desroches et al., 2010). Activation of the left vOT during speech processing is task and stimuli dependent and when the task does not require access to the orthographic representation a specific deactivation was observed instead (Ludersdorfer et al., 2016; Yoncheva et al., 2010).

Blindness as a model for neural plasticity connected to language

As mentioned above, differences in the writing systems (e.g. orthographic transparency) might to some extent affect the relationship between reading and its cognitive correlates. Meanwhile, writing systems can differ also in the reading modality. Blind Braille readers use their sense of touch for reading (Braille, 1839). The Braille alphabet is a writing system as it encodes spoken language. There are multiple Braille alphabets used to encode almost every language spoken. Braille letters and symbols (in non-alphabetic languages) are represented by a combination of one to six raised dots. The 8-dot Braille system is used in some specific situations but is not currently used for the transcription of language (*World Braille Usage.*, 2013). Some Braille alphabets, e.g. English, use contractions in order to save space and increase reading speed (Dodd & Conn, 2000). Contractions are one or two sign symbols replacing a short, frequent word (e.g. AND or THE in English) or units frequent in a given orthography (e.g. TION or EA also in English). Contractions may have an important influence on the cognitive processing of Braille script (Dodd & Conn, 2000; Fischer-Baum & Englebretson, 2016). In Polish, an alphabetic language, every Braille sign encodes one speech sound and has its analogue in the print Latin alphabet used for writing down Polish. The contraction system was also proposed for Polish (Józefowicz & Saloni, 1991) but is not used in education and everyday practice (*World Braille Usage.*, 2013).

Change in the modality of reading from visual to tactile has some inevitable consequences for the cognitive characteristics of Braille reading. Early studies focused on Braille reading were concentrated mainly on the importance of hand movement patterns (Bertelson et al., 1985; Bradshaw et al., 1982; Hermelin & O’Connor, 1971; Wilkinson & Carr, 1987) and haptic factors (Davidson et al., 1992; Semenza et al., 1996). Currently, the consensus is that there is no hand that is better adapted for Braille reading and that individual preference is more important (Garcia, 2004; Paoletti, 1990; Paplińska, 2018). Two-hand strategy is recommended for beginning readers, instead of reading using only one hand (Paplińska, 2018). As a result of repeated practice during Braille processing (and not only visual deprivation, as there are no differences in tactile acuity in other body parts than fingers, Wong et al., 2011), both passive tactile acuity (Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013; Wong et al., 2011) and active tactile acuity (Legge et al., 2008) are enhanced in blind subjects. The relationship between Braille reading and tactile acuity is probably reciprocal, as higher sensitivity to tactile stimuli is positively correlated with Braille reading speed (Stevens et al., 1996; Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013).

Another difference between print and Braille reading is the fact that tactile reading has been shown to be more sequential (Carreiras & Álvarez, 1999; Legge et al., 1999; Mommers, 1976; Perea et al., 2012, 2015; Veispak, Boets, & Ghesquière, 2012; Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013). Letters can be perceived only one by one using the sense of touch and are integrated into words in the process (Simón & Huertas, 1998). However, some kind of supraletter processing must take place during Braille reading. Real words were read faster and more accurately than unknown pseudowords by blind Braille readers (Krueger, 1982; Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013). Word frequency has an influence on Braille reading speed, suggesting word-level and not only sublexical processing during Braille reading (Baciero et al., 2022; Bertelson et al., 1992; Carreiras & Álvarez, 1999). Words in context (in a narrative) are also read more efficiently than presented as nonsensical lists (Mousty & Bertelson, 1985).

When it comes to cognitive correlates of Braille reading and literacy-related skills, studies are much more scarce. Semantic knowledge of visually deprived subjects was shown to be very similar and organized in a comparable way to sighted subjects (Bottini et al., 2022; Canessa et al., 2021; Castonova & Seron, 2007; Kim et al., 2021; Kim & Bedny, 2021; Mikolajczak-Matyja, 2015; Sholl & Easton, 1986) with only slight differences connected to perceptual features of analyzed concepts (e.g. importance of colour for the definitions of natural objects, Connolly et al., 2007, accessibility of different type of perceptual features of objects, Papadopoulos et al., 2017; Vinter et al., 2012). Improvements in auditory processing of both speech (Arnaud et al., 2018; Dietrich et al., 2013; Moos & Trouvain, 2007) and non-linguistic stimuli (Arnaud et al., 2018; Gougoux et al., 2004; Lessard et al., 1998; Muchnik et al., 1991; Röder et al., 1999; Stankov & Spilsbury, 1978) were demonstrated in the blind. Blind subjects were also shown to have better verbal fluency than the sighted subjects (Occelli et al., 2017; Röder et al., 2003; Wakefield et al., 2006 but see Nejati & Asadi, 2010), as well as enhanced verbal short-term memory (Hull & Mason, 1995; Occelli et al., 2017; Pasqualotto et al., 2013; Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013). The latter was suggested to be related to Braille reading efficiency (Millar, 1990; Papastergiou & Pappas, 2019).

Differences in PA between blind and sighted were tested in only a few studies and the results of such comparisons were mixed. The sequential nature of reading and reliance on the grapho-phonological strategy of reading could improve the capacity to manipulate speech sounds, however, only one study has demonstrated an advantage in PA tests in blind subjects compared to sighted (Greaney & Reason, 1999). Other studies either did not find any differences between the two groups (Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013) or have found better PA skills in sighted subjects (Dodd & Conn, 2000). Differences between the studies may be to some extent explained by differences in the alphabet, notably the use of contractions. Sighted participants were shown to be more skilled in the PA test in a study with English-speaking participants, whereas no differences between blind and sighted were shown in Dutch and Estonian populations, which use uncontracted alphabets.

The direct relationship between Braille reading and other cognitive skills usually associated with successful print reading development was studied only in two experiments, spanning the Estonian and Dutch Braille readers populations (Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013). Both studies have confirmed that blind Braille readers were slower in reading but not less accurate than sighted print readers. The authors did not find differences in the level of PA skills in either of the populations. In both populations, the level of PA skills was also significantly correlated with Braille reading efficiency. RAN turned out to be another reading correlate present in both groups. Conversely, verbal short-term memory, as well as tactile acuity, were significantly related to reading only in the blind group.

Changes to the spoken language network

Visual deprivation induces changes not only to the modality of reading, and by consequence, to its behavioural correlates to some extent. The occipital cortex, in the sighted engaged in visual processing, in the blind does not receive this kind of primary sensory input. Studying the consequences of blindness enables us to observe changes in the neural organisation of an evolutionary old system like the spoken language network, as well as to examine the influence of the change in the modality in a relatively new cognitive skill - reading.

The neural network for spoken language processing largely overlaps in blind and sighted. Language processing also activates perisylvian temporal and frontal areas in the blind (Bedny et al., 2011, 2015; Burton, Snyder, Diamond, et al., 2002; Hertrich et al., 2009; Struiksma et al., 2011). It seems that the organisation of the network is also similar: the regions active during phonological (Arnaud et al., 2013; Burton et al., 2003) and semantic processing (Bedny, Caramazza, et al., 2012; Burton et al., 2003; Handjaras et al., 2016; Noppeney et al., 2003; Peelen et al., 2014; Striem-Amit et al., 2018) are very similar when blind and sighted subjects are compared. Some studies reported that the leftward lateralization of the language network may be diminished following visual deprivation (Röder et al., 2000, 2002), while others reported mainly a left-lateralized network also in the blind (Bedny et al., 2011; Noppeney et al., 2003). Two studies that have analysed the lateralization of the language network in the blind in the quantitative way demonstrated a decrease in left hemisphere dominance (Lane et al., 2017; Pant et al., 2020).

The most significant difference between the language networks of blind and sighted is the involvement of the occipital cortex for speech processing. The occipital cortex of the blind is involved in many high-order cognitive processes like verbal memory (Amedi et al., 2003), shape recognition (Pietrini et al., 2004), spatial processing (Collignon et al., 2011), and also in Braille reading (Büchel, Price, & Friston, 1998; Sadato et al., 1996). Sensitivity of the occipital areas to cognitive processes other than vision was shown to be influenced by the age of onset of blindness. In late-blind individuals, occipital activity during cognitive tasks is less extensive and less specialised (Bedny, Pascual-Leone, et al., 2012; Burton, Snyder, Diamond, et al., 2002; Pant et al., 2020).

The occipital cortex activity specific to language (over attentional or memory-related parts of the linguistic tasks) was observed in the blind (Amedi et al., 2004; Lane et al., 2015; van Ackeren et al., 2018) and it was shown to be spatially separated from other functions (Kanjlia et al., 2021). The language-related activity was observed not only in primary visual areas but also in higher-order regions. Notably, the vOT cortex was shown to be active during speech processing in the blind. This activation was related to syntactic processing (Kim et al., 2017), but some studies suggest that it may also be implicated in phonological processing. Arnaud et al., 2013 found a repetition suppression effect during spoken vowels presentation in the vOT and Burton et al., 2003 observed activation in the vOT during the auditory rhyming task.

The blinds' occipital cortex seems to have altered connectivity with other brain regions. The connectivity with prefrontal and temporal areas seems to be strengthened (Abboud & Cohen, 2019; Kanjlia et al., 2021). What is important though, the observed changes in the connectivity were mainly tracked using functional and not structural measures. The structural white matter connections probably stay unchanged (Noppeney, 2007) or may be depleted to some extent following the visual deprivation (Anurova et al., 2019; Ptito et al., 2008; Reislev et al., 2016; although see: Bauer et al., 2017).

Changes to the reading network

Though Braille reading was tested at the beginning of the imaging studies that examined language-related activation in the blind, the attention was focused mainly on primary visual areas (Sadato et al., 1996) and the vOT. Braille reading was shown to activate the classical print reading network (Burton, Snyder, Conturo, et al., 2002), however, the most discussed finding was the activation of the vOT cortex during Braille reading (Büchel, Price, & Friston, 1998; Büchel, Price, Frackowiak, et al., 1998). For a long time, it was mainly the early visual areas' role in Braille reading that was thoroughly analysed and discussed. It was shown that the occipital responses to Braille are not an effect of touch-related activity (Gizewski et al., 2003) and they were shown to be specific and separable from other cognitive functions (Amedi et al., 2003). The region selectively activated by exposition to letters and words in the left vOT was later shown to be in close proximity in the blind and sighted populations (Reich et al., 2011). However, the exact function of the vOT during Braille reading remains controversial. Repetition suppression effects during the presentation of tactile letters, but not speech sounds were shown in this region (Rączy et al., 2019). On the other hand, syntactic complexity of the spoken sentences was shown to modulate the activity of the individually localised letter-sensitive region in the blind, but not in the sighted (Kim et al., 2017). Recently, blinds' vOT was shown to be lacking the typical posterior-to-anterior gradient, which is characteristic of the reading-sensitive region in the vOT of sighted subjects (Tian et al., 2022). The posterior-to-anterior gradient is the proposed organisational principle observed in vOT of sighted readers (Vinckier et al., 2007). The activation related to written stimuli increases with their complexity along the posterior-to-anterior axis, with letters activating the posterior vOT most and word stimuli peaking in the anterior vOT. In the blind, this pattern of activation was found to be absent in the vOT (Tian et al., 2022). Instead, the posterior parietal cortex was shown as a candidate region for the orthographic representations storage in the blind Braille readers.

Only a few studies analysed the neural activations during single word reading in Braille and focused on the areas outside the occipital cortex. Even more scarce are the studies focusing only on "passive" Braille reading, without any additional linguistic task (e.g. verb generation). All of the studies focusing on Braille reading recruited adult subjects, blind children were studied only during spoken language processing (Bedny et al., 2015; Lane et al., 2017). Studies taking a closer look at the Braille reading network in children are lacking. What is more, no study up to date looked into the overlap of the functional networks processing spoken and written language in the blind.

Cross-modal plasticity theories

The changes to the language networks of visually deprived participants are interpreted in the context of more broad theories of neural plasticity and especially cross-modal plasticity - studying the limits of modality dominance over a given region (e.g. visual dominance in the occipital cortex). The two leading theories are the Task Selectivity Sensory-Independent principle (Amedi et al., 2017) and the Pluripotent Cortex Hypothesis (Bedny, 2017).

The Task-Selective Sensory Independent theory states that the functional specialisation of a given brain region depends on the innate computational characteristics of the area rather than on the access to specific sensory information. Studies showing similar specialisation for the same cognitive tasks completed using different modalities in the sensory-deprived population are treated as arguments supporting this theory. An example of such a study is an experiment showing that deaf participants process visual rhythm information in the same anatomical region as the hearing subjects processing auditory stimuli (Bola et al., 2017). The authors of the Task-Selective Sensory Independent hypothesis state that despite the preservation of the large-scale connectivity patterns within a specialised network (e.g. language network), functional connectivity between the early sensory regions and high-order areas may be subject to adaptation to the task demands. Similarities between the network organisation in the deprived and non-deprived populations are interpreted as stemming from the task demands similarities that persevere despite the changed modality of the task.

The Pluripotent Cortex Hypothesis, on the other hand, assumes that the functional specialisation of a given brain area is the effect of the experience that is dependent on the connectivity patterns between the given region and other brain areas. It is the kind of input into the given location that determines the functional specialisation of the region. The theory assumes the preservation of the connectivity patterns - both structural and functional. The existing connections may though become uncovered or strengthened due to the changed input to a given region. At birth, the human cortex is pluripotent - capable to assume different cognitive functions, however, innate computational predispositions are not excluded by this theory. The best-documented example of the pluripotency mechanism at work is the functional specialisation of the occipital cortex in the blind population (Bedny, 2017). As the visual input from the thalamus is abolished, the connectivity of the occipital cortex with the frontoparietal higher-order regions becomes the source of input. These new inputs change the functional specialisation of the occipital cortex. Thus, even if similarities between the networks of deprived and non-deprived populations are observed they may not be an effect of the same computational properties of studied regions but rather of the connectivity between the preserved high-order functional networks.

Original Study

Rationale

The question about the sources of the functional organisation of the human brain is inevitably entangled with the question about neural plasticity. The developmental paths of different cognitive skills and their localization in the human brain can be placed on a continuum spanning processes that are evolutionary old, developing mainly according to innate trajectories to skills completely new in the human cognitive repertoire that find neural niches while being learned. Studying visual deprivation and language in its different forms gives the opportunity to test the effects of environmental changes on the development of skills from the two ends of this spectrum. First, we can ask a question about the influence of blindness on the largely innate spoken language network. The modality for processing spoken language remains unchanged in blind individuals, the language structure also stays the same. Nevertheless, it was already shown before that the functional organisation of the language network is not indifferent to the lack of visual input - occipital areas become recruited for processing language.

Secondly, we can ask how the changes in the spoken language network along with the change in the modality used for reading influence the neural reading network. Though Braille reading-related activity has been studied since the beginning of brain imaging studies, detailed characterisation of the reading network in the blind is still lacking. What is more, speech-reading convergence was not studied in the blind population despite the importance of this phenomenon to the development of reading skills and neural organisation of the reading network.

Lastly, previous studies that looked for the differences between the cognitive correlates of Braille and print reading, were rare and based on quite small samples ranging from 13 to 30 participants per group. Often they were conducted on English-speaking Braille readers and thus on the script that uses contractions. The examination of the cognitive correlates of Braille reading in an orthography that is linguistically completely parallel to the visual script used in the population using the same spoken language is still rare and may bring interesting insights into similarities and differences induced by reading modality. Also, little is known about the development of Braille literacy skills.

These questions were tackled in the course of preparation of this thesis. The precise research questions and hypotheses will be described in the next chapters along with the summary of separate studies that tried to answer them. Study 1 contains the description of the results that were already published in a Dzięgiel-Fivet et al., 2021 paper.

Participants

Fifty-five blind (mean age = 23.08, SD age = 13.81, range: 6.76 – 60.32, 31 female, Table 1) and 54 sighted (mean age = 22.97, SD age = 13.45, range: 6.79 - 59.83 years, 31 female, Table 2) participants were recruited in a scientific project focused on the behavioural and neural correlates of Braille literacy in the blind (Sonata BIS grant number 2016/22/E/HS6/00119 financed by the National Science Centre). Blind children were recruited in schools offering special education adapted for children with visual disabilities and through the Internet (websites and forums for parents of children with disabilities). The recruitment took place from September 2017 to June 2021. Blind adults were recruited via a mailing list for people with visual disabilities managed by the Office for Persons with Disabilities of the University of Warsaw (https://bon.uw.edu.pl/uslugi/typhlos-lista-dyskusyjna-osob-niewidomych-i-slabowidzacych/). Participants of previous studies conducted in the Laboratory of Brain Imaging were also contacted and some were recruited. Adult blind subjects were recruited between April 2018 and October 2019. The blind group was of convenience - all of the volunteers matching the inclusion criteria (early blindness - blindness before the onset of Braille reading acquisition, Braille as primary script for reading acquisition, no knowledge of print Latin alphabet) were tested. Sighted children were recruited in Warsaw schools. Sighted adult participants were recruited mainly through an Internet announcement published on Facebook. Out of the sighted volunteers, participants were chosen to ensure matching to the blind group in terms of age, sex and handedness.

The blind subjects started Braille reading acquisition between the age of 6 and 9. Adult participants were asked to self-assess the level of their Braille reading skills and most declared average, good or very good Braille reading level. A single participant judged her Braille skills as poor (ABF08, see Table 1). Her reading performance, however, was similar to other blind participants. Forty-five of the blind participants were congenitally blind. Another 10 have lost vision early in development (from 9 months to 6 years). Twenty-one blind participants declared having no residual vision, 16 - minimal light perception, and 4 - minimal light and movement perception. For 14 blind participants data about the residual vision was missing. All of the blind participants were declared legally blind.

Handedness was evaluated using the Polish version of the Edinburgh Handedness Questionnaire (Dragovic, 2004). For most of the participants the right hand was dominant (49 blind, 46 sighted). However, a large group of blind participants declared the preference of their left hand for reading Braille (22 subjects). This is not uncommon, as hand dominance and hand preference for reading often dissociate in the blind (Paplińska, 2018). The study was reviewed and accepted by the Scientific Studies Ethics Committee of the Institute of Psychology, Jagiellonian University, which applies The Declaration of Helsinki rules. Adult participants gave informed consent at the beginning of the experimental session. The consent form was beforehand presented to the blind participants in a screen reading software readable format. In the case of minor participants, the written consent was given by the parents and the verbal consent of the children was acquired.

Table 1. Demographic information on the blind participants. Abbreviations: F - female, M - male, R - right hand, L - left hand, NA - not applicable, ND - no data. Age, blindness onset, Braille reading acquisition onset given in years.

Code	Age	Sex	Handedness	Study 1	Study 2	Study 3	Words/Min.	Blindness Onset	Blindness Cause	Reading Hand	Braille Self-assesment	Residual Vision	Braille Reading
ABF01	35.45	F	R	yes	yes	yes	93.43	0	Eyeballs cancer	R	very good	None	7
ABF02	36.36	F	R	yes	yes	yes	63.48	0	Retinopathy of prematurity	L	very good	Light perception	7
ABF03	30.29	F	R	yes	yes	yes	50.30	0	Retinopathy of prematurity	L	very good	Light perception	7
ABF04	44.13	F	R	yes	yes	yes	52.06	0	Congenital rubella syndrome	R	very good	None	7
ABF05	47.96	F	R	yes	yes	yes	54.39	0	Unknown	L	average	None	7
ABF06	36.85	F	R	yes	yes	yes	44.59	0	Glaucoma	R	good	None	7
ABF07	31.02	F	R	yes	yes	yes	25.43	0	Leber's congenital amaurosis	R	average	Light perception	7
ABF08	18.99	F	R	yes	yes	yes	43.63	2	Retinoblastoma	R	poor	None	6
ABF09	27.78	F	R	yes	yes	yes	56.43	0	Leber's congenital amaurosis	L	very good	Light perception	6
ABF10	38.70	F	R	yes	yes	yes	48.00	3	Mechanical damage	R	good	None	7
ABF11	41.70	F	R	yes	yes	yes	111.43	0	Retinopathy of prematurity	R	very good	None	9
ABF12	60.32	F	R	yes	yes	yes	63.80	0	Retinopathy of prematurity	R	very good	None	7
ABF13	41.30	F	R	yes	yes	yes	65.30	0	Leber's congenital amaurosis	R	good	Light and movement perception	7
ABF14	24.03	F	R	yes	yes	yes	52.98	0	Congenital rubella syndrome	R	average	None	7
ABF17	28.21	F	L	yes	yes	yes	63.84	0	Optic nerve hypoplasia	R	good	None	6
ABF18	45.18	F	R	yes	yes	yes	70.34	0	Retinopathy of prematurity	L	very good	None	7
ABM01	37.84	M	R	yes	yes	yes	76.02	0	Optic nerve hypoplasia	R	very good	Light and movement perception	7
ABM02	46.10	M	R	yes	yes	yes	44.75	0	Optic nerve hypoplasia	L	average	Light perception	7
ABM03	35.74	M	R	yes	yes	yes	26.18	0	Unknown	L	good	None	7
ABM04	21.00	M	R	yes	yes	yes	78.04	0	Retinopathy of prematurity	L	good	Light perception	7

Code	Age	Sex	Handedness	Study 1	Study 2	Study 3	Words/Min.	Blindness Onset	Blindness Cause	Reading Hand	Braille Self-assesment	Residual Vision	Braille Reading
ABM05	37.76	M	R	yes	yes	yes	56.59	0	Retinitis pigmentosa	R	good	Light and movement perception	8
ABM06	52.43	M	R	yes	yes	yes	50.45	0	Cataract, glaucoma	L	very good	None	7
ABM07	19.39	M	R	yes	yes	yes	44.46	0	Bilateral microphthalmia	L	average	Light perception	6
ABM08	27.06	M	R	yes	yes	yes	53.85	0	Retinopathy of prematurity	R	average	Light and movement perception	7
ABM09	36.18	M	R	yes	yes	yes	93.38	0	Retinopathy of prematurity	L	very good	Light perception	6
LBF01	10.45	F	R	no	yes	yes	4.17	0	Unknown	R	NA	ND	7
LBF02	9.22	F	R	no	yes	no	42.60	3	Unknown	R	NA	ND	7
LBM01	10.01	M	R	no	yes	yes	27.72	ND	Optic chiasm cancer	L	NA	Light perception	7
LBM03	6.76	M	R	no	yes	no	12.87	0	Leber's congenital amaurosis	L	NA	ND	6
LBM04	9.59	M	R	no	yes	yes	14.79	0	Leber's congenital amaurosis	L	NA	Light perception	7
CBF301	9.28	F	L	no	yes	yes	16.97	0	Retinoblastoma	L	NA	ND	7
CBM301	9.75	M	L	no	yes	yes	32.50	2	Retinoblastoma	L	NA	None	7
CBF401	10.48	F	R	no	yes	yes	54.13	2	Retinoblastoma	L	NA	ND	7
CBM401	10.24	M	R	no	no	yes	28.94	0	ND	ND	NA	ND	7
CBM402	12.83	M	R	no	yes	yes	21.61	0	Retinopathy of prematurity	R	NA	Light perception	7
CBF501	11.81	F	L	no	yes	yes	10.89	0	Optic nerve hypoplasia	L	NA	None	7
CBF502	11.21	F	R	no	yes	yes	31.67	0	Optic neuritis	L	NA	ND	7
CBF503	11.92	F	R	no	yes	yes	33.27	0	Leber's congenital amaurosis	R	NA	None	7
CBM503	12.51	M	R	no	yes	yes	27.65	0	Unknown	L	NA	ND	7
CBF602	12.95	F	R	no	yes	yes	24.94	0	Retinopathy of prematurity	R	NA	None	7
CBF603	13.21	F	R	no	yes	yes	55.77	0	Retinopathy of prematurity	R	NA	Light perception	7
CBF607	13.26	F	R	no	yes	yes	52.52	0	Unknown	R	NA	None	7

Code	Age	Sex	Handedness	Study 1	Study 2	Study 3	Words/Min.	Blindness Onset	Blindness Cause	Reading Hand	Braille Self-assesment	Residual Vision	Braille Reading
CBM601	13.06	M	L	no	yes	yes	35.46	0	Anophthalmia	L	NA	None	7
CBM602	11.52	M	R	no	yes	yes	27.35	2	Retinoblastoma	R	NA	ND	7
CBM603	12.39	M	R	no	no	yes	53.45	0	ND	ND	NA	ND	7
CBM701	15.11	M	R	no	yes	yes	48.98	0	Retinopathy of prematurity	R	NA	Light perception	7
CBF302	11.34	F	L	no	yes	yes	14.50	0	Retinopathy of prematurity	L	NA	ND	7
CBF404	9.47	F	R	no	yes	yes	18.18	0	Optic nerve hypoplasia	R	NA	ND	7
CBM604	13.03	M	R	no	yes	yes	29.24	0.83	Retinoblastoma	R	NA	ND	7
CBM801	14.99	M	R	no	no	yes	69.80	ND	ND	R	NA	Light perception	7
CBF1001	16.30	F	R	no	yes	yes	66.52	6	Glaucoma	R	NA	Light perception	7
CBF1002	18.51	F	R	no	yes	yes	36.99	0	Retinopathy of prematurity	R	NA	None	7
CBF1003	16.98	F	R	no	yes	yes	66.45	0	Retinopathy of prematurity	R	NA	Light perception	7
CBM1001	17.72	M	R	no	yes	yes	58.26	0	Unknown	R	NA	None	7
CBM302	11.48	M	R	no	no	yes	34.78	0	Anophthalmia	ND	NA	ND	7

Table 2. Demographic information on the sighted participants. Abbreviations: F - female, M - male, R - right hand, L - left hand, NA - not applicable, ND - no data. Age given in years.

Code	Age	Sex	Handedness	Study 1	Study 2	Study 3	Words/Min.
ACF03	30.24	F	R	yes	yes	yes	135.00
ACF04	44.66	F	R	yes	yes	yes	97.50
ACF05	45.41	F	R	yes	yes	yes	85.50
ACF07	30.56	F	R	yes	yes	yes	83.63
ACF08	19.68	F	R	yes	yes	yes	116.25
ACF10	37.59	F	R	yes	yes	yes	100.50
ACF14	24.09	F	R	yes	yes	yes	123.00
ACF11	41.76	F	R	yes	yes	yes	150.00
ACF06	37.48	F	R	yes	yes	yes	116.25
ACF12	59.83	F	R	yes	yes	yes	138.13
ACF02	37.64	F	R	yes	yes	yes	129.38
ACF09	26.92	F	R	yes	yes	yes	140.00
ACF13	41.83	F	R	yes	yes	yes	140.63
ACF17	28.34	F	L	yes	yes	yes	131.25
ACF18	45.74	F	R	yes	yes	yes	102.75
ACF19	36.63	F	R	yes	yes	yes	96.75
ACM04	21.74	M	R	yes	yes	yes	120.00
ACM05	35.27	M	R	yes	yes	yes	121.50
ACM08	27.87	M	R	yes	yes	yes	120.00
ACM03	33.65	M	R	yes	yes	yes	116.25
ACM10	38.05	M	R	yes	yes	yes	146.25
ACM12	32.15	M	R	yes	yes	yes	135.00
ACM11	36.07	M	R	yes	yes	yes	146.25
ACM07	19.10	M	R	yes	yes	yes	108.00
ACM06	52.27	M	R	yes	yes	yes	79.50
CCM402	9.04	M	R	no	yes	yes	85.50

Code	Age	Sex	Handedness	Study 1	Study 2	Study 3	Words/Min.
CCF401	10.06	F	R	no	yes	yes	101.25
CCF502	10.77	F	R	no	yes	yes	84.88
CCF503	11.50	F	R	no	yes	yes	99.43
CCF602	13.12	F	R	no	yes	yes	75.11
CCM602	11.96	M	R	no	yes	yes	120.00
CCM403	9.65	M	R	no	yes	yes	94.43
CCF514	11.53	F	R	no	yes	yes	91.13
CCM601	12.98	M	L	no	yes	yes	87.93
CCM301	9.57	M	L	no	yes	yes	55.27
CCM615	12.37	M	R	no	yes	yes	95.25
CCF315	9.58	F	R	no	yes	yes	59.36
CCF515	10.35	F	R	no	yes	yes	120.00
CCM501	10.96	M	L	no	yes	yes	112.50
CCM604	12.98	M	R	no	yes	yes	135.00
CCM302	10.14	M	R	no	yes	yes	90.43
CCF303	8.97	F	R	no	yes	yes	30.38
CCF304	9.29	F	R	no	yes	yes	62.00
CCM303	9.99	M	L	no	yes	yes	63.04
CCM701	13.74	M	R	no	yes	yes	95.25
CCF701	14.26	F	R	no	yes	yes	116.25
CCF802	14.80	F	L	no	yes	yes	84.75
CCF801	15.03	F	L	no	yes	yes	120.00
LCM102	6.79	M	R	no	yes	no	26.14
CCF1001	16.73	F	R	no	yes	yes	103.13
CCF1002	17.15	F	ND	no	yes	yes	100.50
CCF1003	17.20	F	R	no	yes	yes	118.13
CCM1001	17.13	M	R	no	yes	yes	127.50
CCM1002	18.17	M	R	no	yes	yes	87.50

Tasks and Measures

During the experimental sessions, subjects went through a battery of behavioural tests (Study 3) and took part in MRI scanning (Studies 1 and 2). For clarity, measures analysed in every study are described separately.

The scanning sessions took place in the Laboratory of Brain Imaging of the Nencki Institute of Experimental Biology in Warsaw. The data were collected on the 3T Siemens Trio Scanner. The functional sequences used for the collection of the data analysed in each experiment, as well as analysis details are described together with the description of the paradigm used. All of the visual stimuli were presented on an LCD screen, auditory stimuli were displayed using noise-attenuating headphones (NordicNeuroLab), while tactile stimuli via NeuroDevice Tacti TM Braille display (Debowska et al., 2013). The tasks for the functional scanning were designed and presented using the Presentation Software (Neurobehavioral Systems, Albany, CA). The anatomical data were obtained 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).

Study 1

Research questions and hypotheses

The first experiment aimed at mapping the spoken and reading neural networks in the blind population and comparing them to the organisation of language processing in the sighted. As testing for the speech-reading convergence in the blind was lacking in the previous literature we wanted to see whether this phenomenon extends across modalities used for reading. We expected to see a great overlap between the spoken language network in the blind and the sighted. We expected the differences to be present mainly in the occipital cortex, as it was previously reported to be engaged in linguistic processing in the blind. When it comes to the reading network, we also hypothesised that the blind and sighted populations' organisation will be similar - especially in the spoken language processing areas. In the case of the vOT, we wanted to replicate Reich et al. 2011 results through the analysis of the peaks of the individual, reading-related activation. The Reich et al. 2011 study compared participants that were completing different tasks and were scanned in different places. Thus, the replication of these results seemed important. As for the reading network as a whole, we anticipated the occipital cortex to be specifically (more than just sensory activation) involved in Braille reading in the blind. We also awaited some reading-related activity in the somatosensory cortex of the blind group, however, we hypothesised that it will not be reading-specific. Consequently, we expected the speech-reading convergence to be present in the blind, in similar regions as in the sighted - temporal and frontal perisylvian regions.

Participants

Data from adult participants were included in the first study, as the analyses were conducted after the end of the recruitment of the adult participants. Thus, the group consisted of 25 blind (mean age: 35.71, *SD* = 10.08, 16 females) and 25 sighted (mean age: 35.42, *SD* = 9.68, 16 females) participants. Twelve of the blind participants declared some residual vision. One participant per group was left-handed, and the majority of the participants in both groups were right-handed. Eleven blind participants preferred the left hand for Braille reading. Two of the blind subjects were early and not congenitally blind. Both have lost sight before the third year of life. As the age of blindness onset can influence the functional organisation of the brain (Bedny, Pascual-Leone, et al., 2012; Burton, Snyder, Conturo, et al., 2002) the analyses were conducted also without the early blind individuals. The results of these analyses are reported in the Appendix. The differences between the congenitally only and the complete sample were minor.

fMRI task

In Study 1 data from the modified fast language localizer (Chyl et al., 2018; Malins et al., 2016) were analysed. The data were collected in 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 subjects were presented with stimuli in three conditions: real words, pseudowords and non-linguistic control stimuli. Blind participants were presented with auditory and tactile stimuli, and the sighted - with auditory and visual stimuli. The auditory stimuli were recorded with speech-synthesiser using a female voice.

In the real words condition, short (3-4 letters) words consisting of 1 or 2 syllables were presented. The number of adjectives, verbs, and nouns of comparable frequency was balanced. In the pseudowords condition, pronounceable stimuli were created by transposition or substitution of letters in the real words. The form of the control non-linguistic stimuli depended on the modality of presentation. Three or four six-dot Braille signs (⠿ unmeaningful symbol in the Polish Braille alphabet) were used as the tactile control stimuli. To match tactile stimuli in complexity 3 or 4 hash symbols (### or ####) were used as the visual control stimuli. In the auditory modality, the control stimuli consisted of vocoded 1 or 2-syllable words. The word stimuli were vocoded using Praat (www.praat.org). Praat vocoding method divides the signal into 3 frequency bands, applies the dynamic amplitude contour of the original to a noise source, and then recombines these into a unitary signal again. The resulting stimuli have the same physical properties as the original input (dynamic frequency and amplitude) but have no linguistic (phonetic) meaning.

The localizer task was divided into three runs, each consisting of 36 blocks (18 auditory, 18 in the modality appropriate for reading). In a run, there were 6 blocks per condition (real words, pseudowords, control). Each block contained 4 different stimuli from the given condition, presented one after the other. Tactile stimuli were presented for 3000 ms (Kim et al., 2017; Veispak, Boets, Männamaa, et al., 2012), while auditory and visual stimuli were displayed for 1000 ms. The interstimulus interval lasted for 1000 ms. The interblock breaks were 3000 to 6000 ms long.

Data Analysis

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 normalisation of the functional data to the MNI space was carried out with the 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 General Linear Model (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 was rejected. The blocks of six conditions were convolved with canonical haemodynamic function. The contrasts pertinent for the analyses were first created in the first-level analysis. The first-level contrasts were then submitted to the second-level analyses to delineate group-level activations and compare the groups.

Whole-brain analyses

Language-related activations were analysed using two different types of contrasts. Word sensitive (words > baseline, baseline understood as unmodelled rest) contrast was used to delineate brain regions sensitive to linguistic processing, therefore including areas involved in sensory processing of the stimuli. Word-specific (words > non-linguistic control stimuli) contrast was used to identify regions specialised in linguistic processing – not only activated by physical characteristics of the perceived stimuli but involved in higher-order processes. The choice of conditions was adapted to the goal of mapping the reading network in both populations. 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, Kossowski, et al., 2021; Marks et al., 2019; Preston et al., 2016). In order to compare automatized whole-word reading and activation related to sequential reading, the pseudowords > words contrasts were also tested. The comparison of words and pseudowords conditions in the auditory modality was not very informative as both of these conditions have similar phonological content. Conjunction analysis approach (null conjunction, Friston et al., 2005) was used to mark areas activated by both visual and Braille reading. 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 structures within the clusters were labelled using AAL3 atlas (Rolls et al., 2020) and the regions contributing more than 50 voxels to the clusters are described in the tables.

Individual peaks analysis

Analyses of individual-level peaks of activation in the left vOT were conducted to account for individual differences in the location of the reading-sensitive activation. Peaks of activations were defined for the reading-specific (words > non-linguistic control) contrasts in both sighted and blind groups. Individual peaks were defined using the method described by Reich et al., (2011). The individual peaks were defined as the local maximum of activation closest to the group level peak of activation with voxelwise $p < 0.01$; $p < 0.05$ FWE cluster corrected within a ROI. The vOT ROIs were 10 mm radius spheres around the literature peaks: the LEX peak from the Lerma-Usabiaga et al., (2018) study and the peak of the vOT activation of spoken words in a blind sample from the Kim et al. study (2017). If finding a peak was impossible at that threshold, cluster correction was omitted or the voxel level threshold was relaxed to $p < 0.03$. Despite lowering the threshold it was not possible to find an activation peak in the left vOT region in two sighted subjects.

Individual peaks were subjected to the k-means clustering method described by Reich et al., (2011) using an algorithm implemented in the scikit-learn Python library. This method forces the division of the points given as input into two clusters so that the distance between the points and the centre of the cluster they belong to is minimised. The distribution of the peaks belonging to each group within the resulting clusters was tested using Pearson's χ^2 test. This was done to examine whether the proportion of the peaks from different groups was different between the clusters. In addition, since the group membership of individual peaks was known, logistic regression was used with x, y and z coordinates as predictors of group identity.

Speech-reading convergence

To study the speech-reading convergence within the 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 conducted to estimate the intersection between the reading and speech-sensitive network (words > baseline, Rueckl et al., 2015). On the individual level, we used two measures - the number of voxels in the individual convergence maps and correlation of the reading-sensitive and speech-sensitive contrasts estimates (Chyl et al., 2018; Chyl, Kossowski, et al., 2021; Marks et al., 2019; Preston et al., 2016). We aimed at conducting the analyses in a manner comparable to previous studies on speech-reading convergence in the sighted population (children - Chyl et al., 2018, 2021; Marks et al., 2019; Preston et al., 2016; adults - Rueckl et al., 2015). All of these studies, in spite of using different tasks (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 reading and speech-related conditions to resting baseline and not to various control conditions. Then, they conducted the conjunction between reading and speech-related contrasts to delineate the convergence regions. Here a similar approach was applied, however, to control for the effects of multisensory processing, we also report the conjunctions of the language-specific conditions (words > non-linguistic control).

On the individual level, analyses were run in literature-based ROIs. The ROIs were 10 mm radius spheres around the peaks of activations reported by Rueckl and colleagues (2015) as regions that have shown both speech-reading convergence and where a significant correlation of reading and speech contrast estimates was present. They spanned the 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 analysed because these regions were reported to be sensitive to speech processing in the blind (Kim et al., 2017) and they emerged in the speech-reading conjunction in the blind group in the whole-brain analyses. The same left vOT ROI as in the individual peaks analyses were used. To create the right vOT ROI, the left hemisphere vOT ROI was flipped onto the right hemisphere. The number of voxels activated by both reading and speech processing was examined in all of the ROIs (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 overlapping activations during reading and speech processing. These ROIs were not included in the following analyses. In most of the sighted participants, we also did not observe any overlap in the left and right vOT ROIs. Nevertheless, the left vOT ROI was still included in the analyses because it was of particular interest due to the whole-brain conjunction results in the blind group. Finally, right STG, left MTG/STG, and left vOT ROIs were considered for the individual convergence analysis. 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). Next, for each subject, the number of voxels significantly activated for such conjunction was estimated in the three ROIs. In order 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 standardised residuals of the regression analysis with the number of 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 to test for the correlation between reading and speech-sensitive activations. The contrast estimate for the given condition (written and spoken words > baseline contrast) was extracted from each ROI in every subject using the MarsBar toolbox (version 0.44, Brett et al., 2002). Afterwards, the correlation analysis with Spearman's *rho* correlation coefficient was conducted with individual subjects' measures. Fisher's r to z transformation was used to compare the correlation coefficients between the groups (Armitage, & 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. Consequently, following Planton et al., 2019, the individual overlaps between reading and speech-specific activity in the vOT were calculated in this group in a post-hoc manner. Individual ROIs specific to reading and speech (word > non-linguistic control contrasts) were created from significantly active voxels (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 $p_{\text{cluster}} < 0.05$). For each subject, the number of voxels overlapping between the reading and speech-specific individual ROIs was counted. The activity of the voxels activated by reading during speech processing was analysed too, also following Planton et al. (2019). 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. To assess whether the speech-related activations were significantly different from zero Wilcoxon signed-rank test was employed.

Functional Connectivity

Task-related functional connectivity with a seed-to-voxel correlation mapping (weighted GLM option) was performed using the CONN Toolbox v.19 (Whitfield-Gabrieli & Nieto-Castanon, 2012). Spatial normalisation of the structural data was conducted in the toolbox, as well as default denoising procedure (combination of aCompCor, regressing out excessive movement as defined by ART toolbox, motion regression, the 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 (the same as in the convergence analyses) was set as a 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 focused only on positive correlations, omitting negative correlations of which interpretation could be unclear.

Results

Whole-brain results

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

Speech processing led to a much broader activation in the blind subjects than in the sighted group (Figure 1, Table 3). For the speech-sensitive contrasts (words > baseline), the blind group activated the occipital cortex including bilateral vOT and the right IFG more than the sighted group (Figure 2, Table 3). Both groups activated the bilateral temporal cortex. The conjunction between the blind and the sighted groups was present in the bilateral temporal cortex (Figure 1, Table 3). No clusters were activated more by the sighted group than by the blind group (Table

3). The blind subjects activated the bilateral temporal regions and left vOT also for the speech-specific contrast (words > non-linguistic control, Figure 1, Table 4). The sighted subjects activated only the temporal cortex (Figure 1, Table 4). Consequently, the left vOT cluster was activated to a larger extent by the blind than by the sighted for the speech-specific contrast (Figure 2) and the conjunction between the groups was found in the bilateral superior and middle temporal gyri (Figure 1, Table 4).

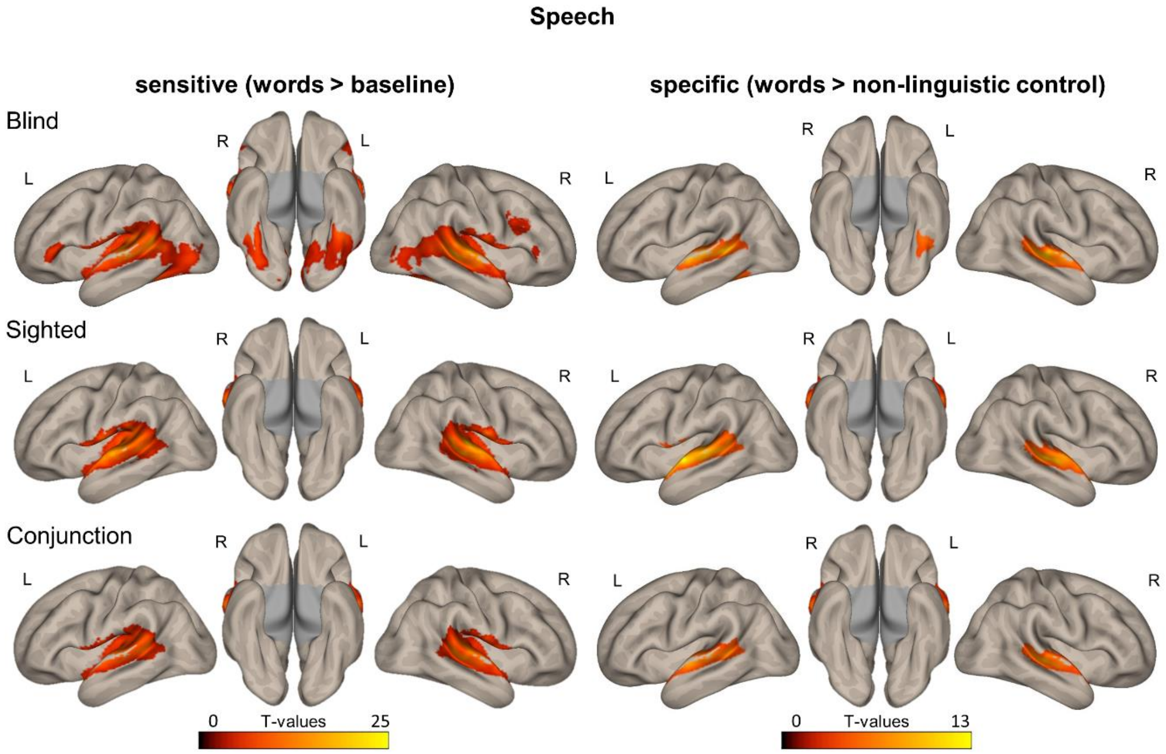

Figure 1. Speech processing related activations in the blind and sighted groups and the conjunction between the groups.

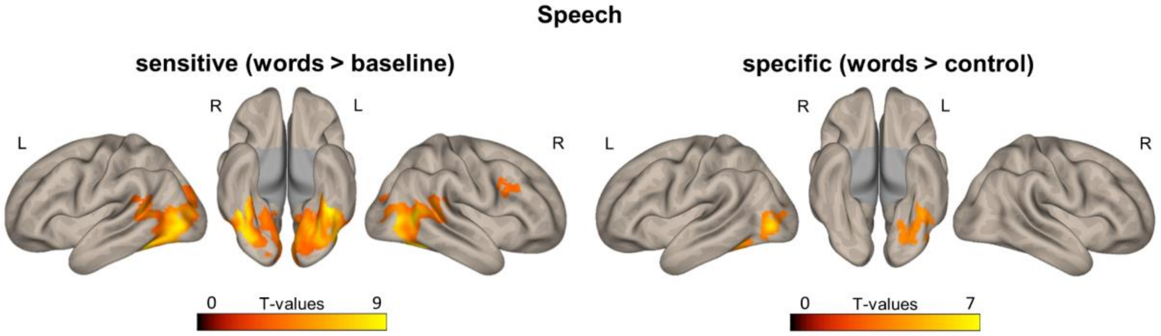

Figure 2. Activations greater in the blind group in comparison to the sighted group in the processing related conditions (words > baseline, words > control). No significant activations greater for the sighted than for the blind.

Table 3. Speech sensitive (words > baseline) activations in the blind and sighted groups, conjunction and differences between the two groups.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Blind							
Superior Temporal Gyrus, Middle Temporal Gyrus, Fusiform Gyrus, Lingual Gyrus, Calcarine, Cerebellum, Inferior Occipital Gyrus, Middle Occipital Gyrus, Rolandic Operculum, Inferior Frontal Gyrus (p. triangularis, orbitalis, opercularis), Inferior Temporal Gyrus, Insula, Heschl Gyrus, Supramarginal Gyrus, Cuneus, Postcentral Gyrus, Angular Gyrus	L	-60	-50	10	20.48	9400	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Fusiform Gyrus, Rolandic Operculum, Infrior Frontal Gyrus (p. triangularis, opercularis, orbitalis), Superior Temporal Pole, Insula, Heschl Gyrus, Cerebellum, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Middle Occipital Gyrus, Supramarginal Gyrus, Postcentral Gyrus	R	62	-12	0	18.07	6302	< 0.001
Inferior Frontal Gyrus (p. triangularis, opercularis), Precentral Gyrus	R	50	18	25	5.87	338	0.016
Sighted							
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Superior Temporal Pole, Insula, Heschl Gyrus, Supramarginal Gyrus	R	60	-24	6	25.17	5138	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Superior Temporal Pole, Insula, Heschl Gyrus, Supramarginal Gyrus, Postcentral Gyrus	L	-58	-26	4	21.49	5445	< 0.001
Blind & Sighted (conjunction)							
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Insula, Superior Temporal Pole, Heschl Gyrus, Supramarginal Gyrus	R	58	-26	4	16.43	4191	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Heschl Gyrus, Superior Temporal Pole, Insula, Supramarginal Gyrus	L	-60	-24	2	15.01	4418	< 0.001
Blind > Sighted							
Lingual Gyrus, Calcarine, Middle Temporal Gyrus, Middle Occipital Gyrus, Fusiform, Inferior Occipital Gyrus, Cuneus, Superior Temporal Gyrus, Cerebellum, Inferior Temporal Gyrus, Superior Occipital Gyrus	L/R	-38	-52	-14	9.33	12555	< 0.001
Inferior Frontal Gyrus (p. opercularis, triangularis)	R	48	20	30	4.54	233	0.035
Sighted > Blind							
No suprathreshold clusters							

Table 4. Speech-specific (words > control) activations in the blind and sighted groups, conjunction and differences between the two groups.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Blind							
Superior Temporal Gyrus, Middle Temporal Gyrus	R	54	-28	2	11.39	1278	< 0.001
Middle Temporal Gyrus, Superior Temporal Gyrus	L	-54	-36	2	10.98	1398	< 0.001
Fusiform Gyrus, Inferior Temporal Gyrus	L	-38	-48	-20	5.83	279	0.048
Sighted							
Middle Temporal Gyrus, Superior Temporal Gyrus, Superior Temporal Pole	L	-58	-6	-4	13.71	2053	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus, Superior Temporal Pole	R	54	-26	-2	11.91	1642	< 0.001
Blind & Sighted (conjunction)							
Superior Temporal Gyrus, Middle Temporal Gyrus, Superior Temporal Pole	R	56	-26	0	10.39	1089	< 0.001
Middle Temporal Gyrus, Superior Temporal Gyrus	L	-58	-24	0	7.82	1259	< 0.001
Blind > Sighted							
Fusiform Gyrus, Middle Occipital Gyrus, Inferior Occipital Gyrus, Lingual Gyrus, Inferior Temporal Gyrus	L	-40	-78	-2	5.93	1108	< 0.001
Sighted > Blind							
No suprathreshold clusters							

In both the sighted and the blind, we observed reading sensitive activations (words > baseline) in the regions typically included in the reading network (bilateral: vOT, precentral/postcentral gyri, IFG; Figure 3, Table 5). The significant conjunction between Braille and visual reading sensitive networks was present in the bilateral vOT. Bilateral occipital clusters (loci of V1/V2), as well as bilateral postcentral gyri and inferior parietal lobule, were activated more by the blind subjects than by the sighted (Figure 4, Table 5). Contrary, bilateral temporal cortices (STG, MTG) and bilateral occipital clusters (inferior occipital gyri) were activated more by the sighted subjects than by the blind (Figure 4, Table 5). The reading-specific contrast (words > non-linguistic control), evoked activation in the bilateral occipital areas, including vOT and in a left frontal cluster (IFG, precentral gyrus, Figure 3, Table 6) in the blind group. The sighted subjects activated the left vOT, left precentral and postcentral gyri in a reading-specific manner. The activation in the bilateral vOT, left calcarine, and bilateral IFG was stronger in the blind than in the sighted subjects (Figure 3, Table 6). In the inverse comparison (sighted > blind) two right hemisphere clusters in occipital and temporal cortices were found. The left vOT was the region of activation overlap between the sighted and the blind.

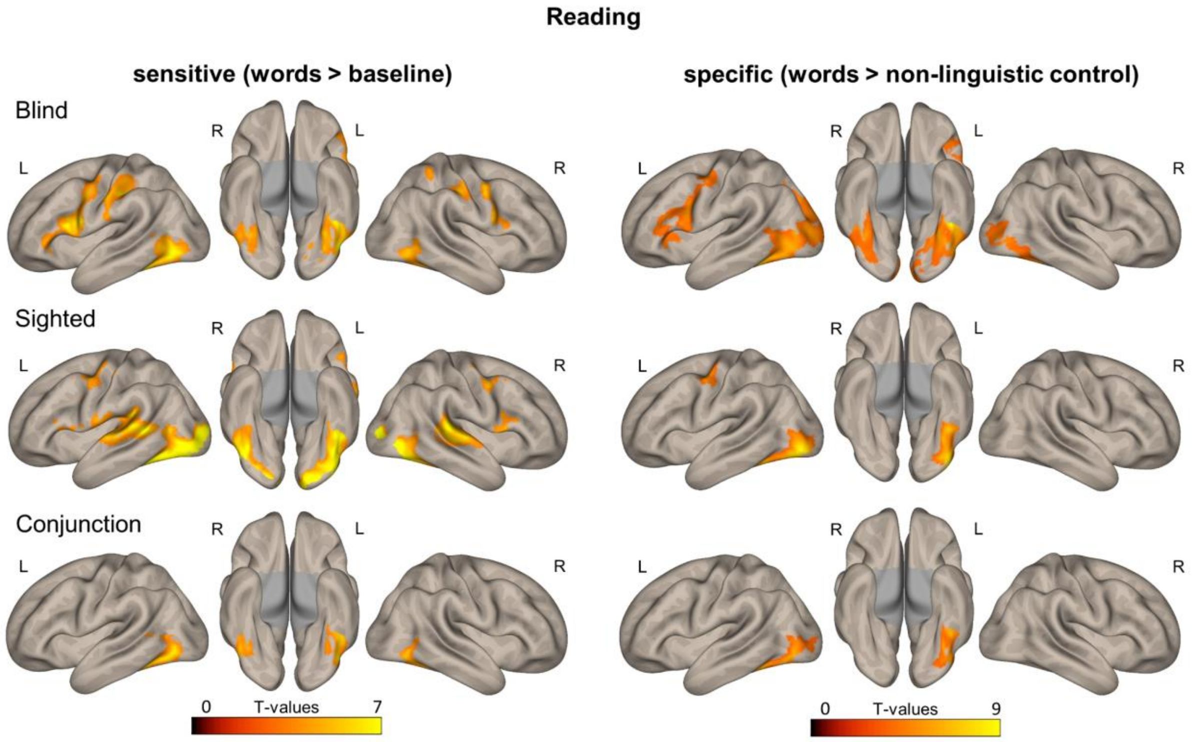

Figure 3. Reading related activations (words > baseline, words > control); blind, sighted & conjunction.

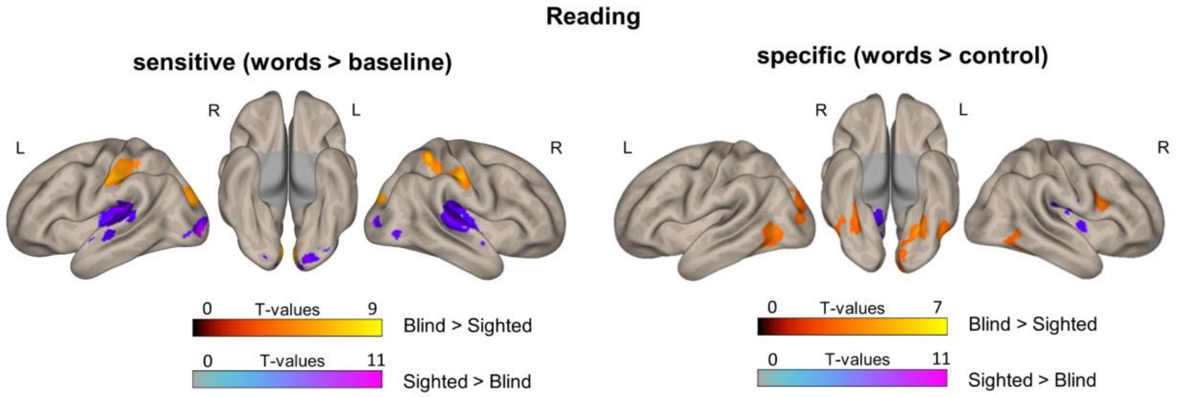

Figure 4. Groups differences in the reading-related activations (words > baseline, words > control).

Table 5. Reading sensitive (words > baseline) activations in the blind and sighted groups, conjunction and differences between the two groups.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
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 Gyrus	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 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
Blind > Sighted							
Cuneus, Calcarine, Superior Occipital Gyrus, Lingual Gyrus, Middle Occipital Gyrus, Cerebellum, Superior Parietal Gyrus	L/R	0	-84	18	7.34	2043	< 0.001
Postcentral Gyrus, Inferior Parietal Lobule, Supramarginal Gyrus, Superior Parietal Gyrus, Precentral Gyrus	R	48	-22	40	6.15	1066	< 0.001
Inferior Parietal Lobule, Postcentral Gyrus, Superior Parietal Gyrus, 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 Gyrus	L	-40	-34	18	7.42	1980	< 0.001
Superior Temporal Gyrus, Insula, Heschl Gyrus, Rolandic Operculum	R	64	-28	10	6.40	1723	< 0.001

Table 6. Reading specific (words > control) activations in the blind and sighted groups, conjunction and differences between the two groups.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Blind							
Middle Occipital Gyrus, Fusiform Gyrus, Superior Occipital Gyrus, Calcarine, Inferior Occipital Gyrus, Cerebellum, Cuneus, Middle Temporal Gyrus, Inferior Temporal Gyrus, Ligual Gyrus, Superior Parietal Gyrus, Inferior Parietal Lobule	L/R	-40	-46	-20	8.79	7254	< 0.001
Inferior Frontal Gyrus (p. triangularis, opercularis, orbitalis), Precentral Gyrus, Insula, Postcentral Gyrus	L	-40	-4	46	5.91	2169	< 0.001
Sighted							
Inferior Occipital Gyrus, Fusiform Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus	L	-40	-80	-10	9.30	1424	< 0.001
Precentral Gyrus, Postcentral Gyrus	L	-50	-4	50	6.38	415	0.003
Blind & Sighted (conjunction)							
Inferior Occipital Gyrus, Fusiform Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus	L	-44	-50	-18	7.01	1109	< 0.001
Blind > Sighted							
Calcarine, Middle Occipital Gyrus, Fusiform Gyrus, Lingual Gyrus, Cerebellum, Middle Temporal Gyrus Inferior Temporal Gyrus, Superior Occipital Gyrus, Inferior Occipital Gyrus, Cuneus	L	-28	-58	-12	6.75	2100	< 0.001
Inferior Frontal Gyrus (p. opercularis, triangularis), Precentral Gyrus	R	44	12	22	5.03	317	0.038
Fusiform Gyrus, Cerebellum, Inferior Temporal Gyrus	R	48	-50	-6	4.77	680	0.002
Inferior Frontal Gyrus (p. opercularis)	L	-46	8	16	4.41	338	0.031
Sighted > Blind							
Lingual Gyrus, Calcarine, Precuneus	R	18	-48	4	5.56	388	0.019
Rolandic Operculum, Insula	R	42	-4	6	4.06	384	0.020

Pseudowords reading evoked activations very similar to words reading in both groups (Figure 5, Table 7). When word reading was directly compared to pseudoword reading, the difference was detected only in the sighted group. The sighted subjects activated bilateral parietal clusters, left IFG and precentral gyrus, and left occipital cluster more during pseudowords reading than during words reading (Figure 6, Table 7). The conjunction of the activations specific to pseudowords reading (pseudowords > non-linguistic control) between the sighted and the blind group included additional regions, to those present in the words > non-linguistic control contrast conjunction such as the left IFG extending to precentral gyrus (Figure 5, Table 7).

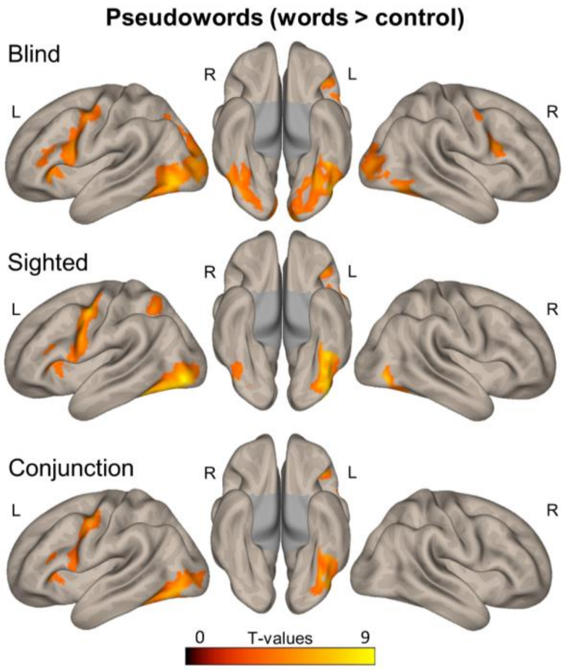

Figure 5. Pseudowords reading specific (pseudowords > control) activations; blind, sighted & conjunction.

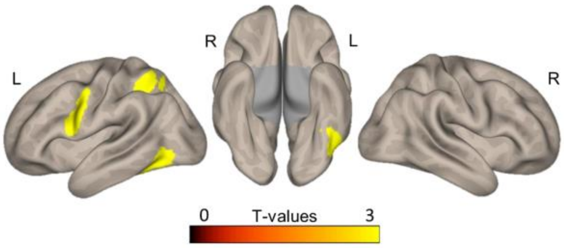

Figure 6. Pseudowords > words activations in the sighted group.

Table 7. Pseudowords reading specific (pseudowords > control) activations in the blind and sighted groups, conjunction.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Blind							
Middle Occipital Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus, Calcarine, Superior Occipital Gyrus, Cerebellum, Lingual Gyrus, Inferior Temporal Gyrus, Middle Temporal Gyrus, Cuneus, Superior Parietal Gyrus, Inferior Parietal Lobule	L/R	-42	-70	-8	7.45	7418	< 0.001
Precentral Gyrus, Inferior Frontal Gyrus (p. triangularis, opercularis, orbitalis), Insula, Postcentral Gyrus	L	-34	28	2	6.32	2113	< 0.001
Inferior Frontal Gyrus (p. opercularis), Precentral Gyrus	R	44	4	24	5.55	625	0.007
Sighted							
Inferior Occipital Gyrus, Fusiform Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus, Cerebellum	L	-40	-80	-8	8.87	1908	< 0.001
Precentral Gyrus, Postcentral Gyrus, Inferior Frontal Gyrus (p.opercularis)	L	-50	-6	50	7.53	1301	< 0.001
Inferior Occipital Gyrus, Inferior Temporal Gyrus, Fusiform Gyrus	R	46	-74	-6	7.46	387	0.004
Supplementary Motor Area	L/R	-4	0	56	6.26	255	0.026
Superior Parietal Gyrus, Inferior Parietal Lobule	L	-24	-54	48	6.13	270	0.021
Inferior Frontal Gyrus (p. triangularis, orbitalis), Insula	L	-38	28	0	6.11	507	0.001
Blind & Sighted (conjunction)							
Inferior Occipital Gyrus, Fusiform Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus, Cerebellum	L	-42	-70	-10	6.87	1512	< 0.001
Precentral Gyrus, Inferior Frontal Gyrus (p. opercularis), Postcentral Gyrus	L	-44	-4	52	5.90	801	0.001
Inferior Frontal Gyrus (p. triangularis, orbitalis), Insula	L	-36	28	0	5.82	387	0.021
Blind > Sighted							
Calcarine, Ligual Gyrus, Superior Occipital Gyrus, Cerebellum, Cuneus, Middle Occipital Gyrus, Fusiform Gyrus	L/R	-8	-94	16	6.47	4208	< 0.001
Sighted > Blind							
No suprathreshold clusters							
Sighted **Pseudowords > words**							
Inferior Temporal Gyrus, Inferior Occipital Gyrus, Fusiform Gyrus	L	-46	-62	-12	8.62	595	< 0.001
Precentral Gyrus, Inferior Frontal Gyrus (p. opercularis)	L	-48	10	16	7.35	818	< 0.001
Inferior Parietal Lobule, Superior Parietal Gyrus	L	-36	-56	56	6.49	893	< 0.001
Inferior Parietal Lobule, Superior Parietal Gyrus	R	32	-62	28	5.01	407	0.003

Individual peak analysis

The peaks from the sighted and the blind subjects were localised in very similar sites. Clustering of the individual activation peaks resulted in clusters that contained peaks from both groups. Six peaks from the blind group fell into cluster one, and 19 into cluster two, whereas 10 peaks from the sighted group fell into cluster one and 13 into cluster two (Figure 7). The difference in the distribution of the peaks from the two groups between clusters one and two measured with Pearson's chi-squared test was not significant ($\chi^2 = 2.05$, $p = 0.153$). In addition, logistic regression analysis showed that the reading-specific individual activation peaks did not differentiate between the sighted and the blind group (for the x coordinate, OR – odds ratio = 0.95, 95% CI: 0.812– 1.10, $p = 0.168$, for the y coordinate, OR = 0.92, 95% CI: 0.83– 1.02, $p = 0.105$, for the z coordinate, OR = 1.04, 95% CI: 0.93– 1.16, $p = 0.496$). The results of the logistic regression models should be treated with caution as the sample size was relatively small for this kind of analysis and the linearity between the logit of outcome and the predictor assumption was not met for one of the predictors (Box-Tidwell test, interaction terms significant and level $p < 0.10$).

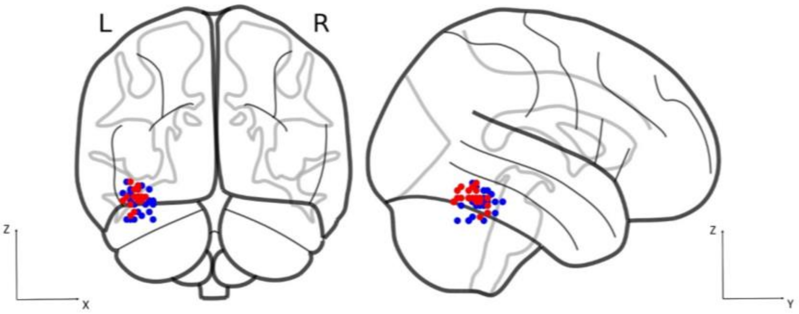

Figure 7. Individual peaks of reading-specific activations (words > non-linguistic control), blue – blind group, red – sighted group.

Speech-reading convergence

The regions of speech-reading conjunctions were different between the blind and the sighted groups (Figure 8, Table 8) for both language-sensitive and language-specific contrasts. In the blind group, conjunction analyses for the language-sensitive contrasts resulted in clusters in the bilateral vOT (extending to MTG in the left hemisphere). Contrary, in the sighted subjects, the bilateral MTG/STG regions presented a significant speech-reading convergence. Individual convergence analysis corroborated these results.

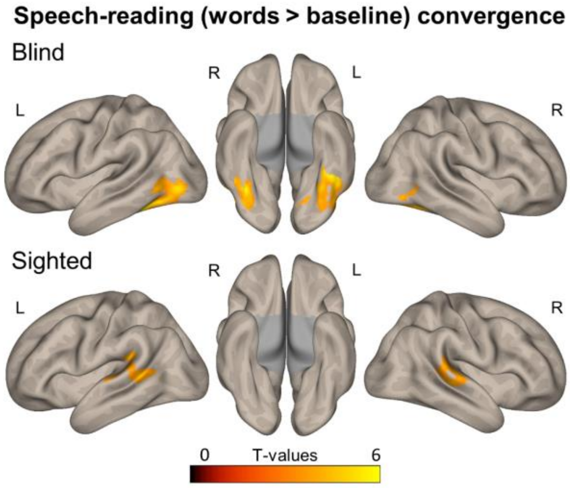

Figure 8. Speech-reading convergence in the blind and sighted groups. Convergence of language sensitive (words > baseline) contrasts.

Table 8. Speech-reading convergence in blind and sighted groups. The language-specific contrasts conjunctions presented without the cluster-level correction.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Language sensitive contrasts (words > baseline)							
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
Language specific contrasts (words > control							
Blind							
Fusiform Gyrus, Inferior Temporal Gyrus, Inferior Occipital Gyrus	L	-40	-46	-20	6.14	311	0.061
Fusiform Gyrus, Inferior Temporal Gyrus, Cerebellum	R	42	-52	-16	5.25	85	0.505
Middle Occipital Gyrus, Inferior Occipital Gyrus	L	-46	-78	4	3.57	52	0.683
Middle Temporal Gyrus	L	-50	-54	2	3.81	51	0.689
Inferior Occipital Gyrus	R	46	-76	-4	3.31	2	0.970
Sighted							
Precentral Gyrus, Postcentral Gyrus	L	-48	-4	52	6.05	164	0.105
Supplementary Motor Area	L/R	-4	-2	62	4.01	118	0.228

As mentioned above, individual convergence was studied using two analytical approaches: counting the number of significant voxels in the individual subject’s conjunction maps (Preston et al., 2016) and correlating the contrast estimates related to reading and speech processing (Rueckl et al., 2015) in specific ROIs (left MTG/STG, right STG, left vOT). Greater convergence, measured as the number of overlapping voxels, was observed in the sighted subjects in the left MTG/STG ($U = 147.00$, $p_{corrected} = 0.004$). The blind subjects presented greater convergence in the left vOT ($U = 180.00$, $p_{corrected} = 0.020$). There was no significant difference between the groups ($U = 226.00$, $p_{corrected} = 0.186$) in the right STG. 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 sighted group. However, in the blind, the only significant correlation was observed 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, $r = 0.68$, $p_{corrected} < 0.001$). When the correlations coefficients in all ROIs were compared between the groups, only the right STG has shown a greater correlation in the sighted (Fisher's $Z = -2.74$, $p_{corrected} = 0.009$). In the two remaining ROIs the group difference did not reach significance (left MTG/STG: Fisher's $Z = -0.60$, $p_{corrected} = 0.548$; left vOT: Fisher's $Z = 0.08$, $p_{corrected} = 0.469$).

When the language-specific (words > non-linguistic control) contrasts were studied to reveal speech-reading convergence, no clusters surviving cluster-level correction emerged in either group (Table 8). In the blind group, the left vOT cluster was on the trend level ($p_{cluster} = 0.061$) and left precentral gyrus activation was additionally present when the results were not corrected at the cluster level.

Speech-reading convergence in the left vOT in the blind

The main region of speech-reading convergence in the blind group turned out to be the left vOT. Post-hoc analyses, following Planton et al. (2019) were thus conducted to explore the nature of speech-related activation in this region. We wanted to know how well separated the reading and speech-processing-related activations are in the left vOT. First, we examined the overlap between individual reading- and speech-specific (words > non-linguistic control) activations 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, $SD = 145.45$). Ten blind subjects did not show any significant left vOT activation for the speech processing contrast and one failed to show activity for the reading contrast (no significant voxels in the volume of search at $p < 0.001$, uncorrected). Thus, only fifteen subjects with 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 accounted for 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.

Then, we tested if the voxels activated by reading are also active during speech processing. We extracted speech-specific contrast estimates from the individual reading-related ROIs (for all, 25 blind subjects). The reading-specific regions turned out to be activated also for speech-specific contrasts ($Z = 271.00$, $p < 0.001$).

Functional connectivity

Functional connectivity of the left vOT with other brain areas was analysed also in a post-hoc manner. In the blind group, the left vOT was activated by both reading and speech processing. This may be a sign of its involvement in language processing independently of the modality. We wanted to know whether in the blind the left vOT belongs to the modality independent language network, contrary to its specialisation for reading observed in the sighted. As functional connectivity is considered to be a measure of network integration (Friston, 2011) we used seed-to-voxel task-related correlation analysis. We compared connectivity during reading and speech processing in both groups. In the blind, there were no differences between the regions correlating with the left vOT in the reading and speech-processing conditions, except for one cluster in the right superior frontal gyrus (Table 9). In the blind, the left vOT proved to be connected with a broad language network (bilateral MTG/STG, inferior frontal and precentral/postcentral gyri), as well as with the occipital cortex (V1/V2 loci, Figure 9, Table 9) independently of the modality of language processing.

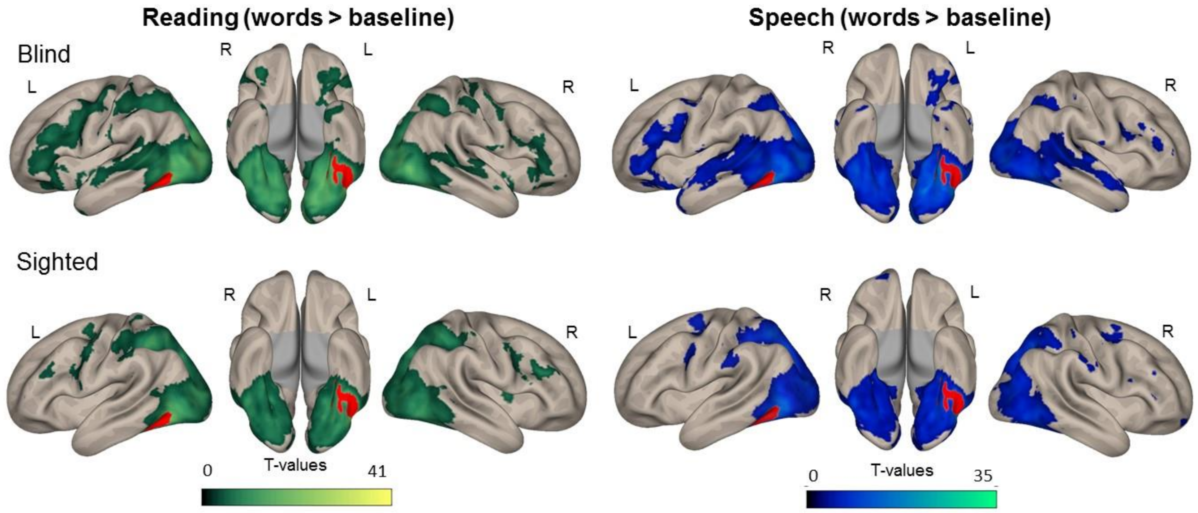

Figure 9. Functional connectivity with the left vOT in the blind and the sighted group during reading and speech processing.

Table 9. Functional connectivity with the left vOT in the blind group during reading and speech processing.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Reading > Speech processing							
Superior Frontal Gyrus, Middle Frontal Gyrus	R	36	60	-8	7.22	197	0.002
Reading-related connectivity							
Middle Occipital Gyrus, Middle Temporal Gyrus, Lingual Gyrus, Calcarine, Fusiform Gyrus, Inferior Frontal Gyrus (p. triangularis, orbitalis, opercularis), Cerebellum, Inferior Parietal Lobule, Superior Occipital Gyrus, Inferior Temporal Gyrus, Inferior Occipital Gyrus, Cuneus, Superior Parietal Gyrus, Postcentral Gyrus, Middle Frontal Gyrus, Precentral Gyrus, Superior Temporal Gyrus, Superior Temporal Pole, Hippocampus, Parahippocampal Gyrus, Amygdala, Putamen, Thalamus, Pallidum, Insula, Middle Temporal Pole, Precuneus, Supramarginal Gyrus	L/R	-36	-54	-10	44.77	58 682	< 0.001
Postcentral Gyrus	L	-52	-12	16	5.88	159	0.022
Precentral Gyrus	R	10	-30	68	4.80	203	0.006
Speech processing related connectivity							
Middle Temporal Gyrus, Middle Occipital Gyrus, Lingual Gyrus, Fusiform Gyrus, Calcarine, Inferior Frontal Gyrus (p. triangularis, orbitalis, opercularis), Cerebellum, Superior Temporal Gyrus, Inferior Temporal Gyrus, Superior Occipital Gyrus, Superior Temporal Gyrus, Inferior Occipital Gyrus, Cuneus, Hippocampus, Superior Parietal Gyrus, Superior Temporal Pole, Parahippocampal Gyrus, Middle Frontal Gyrus, Inferior Parietal Lobule, Precentral Gyrus, Angular Gyrus, Amygdala, Precuneus, Middle Temporal Pole, Insula, Putamen, Supramarginal Gyrus, Thalamus, Postcentral Gyrus, Rolandic Operculum, Heschl Gyrus, Pallidum	L/R	-36	-56	-14	36.68	44 113	< 0.001
Inferior Frontal Gyrus (p. triangularis, opercularis)	R	52	38	18	5.85	822	< 0.001
Precentral Gyrus, Middle Frontal Gyrus	L	-38	-2	64	5.66	353	< 0.001

In the sighted, the activity of the left vOT was correlated with occipital cortex activity, regions in the parietal (inferior parietal lobule) and frontal cortex (IFG, precentral/postcentral gyri, Figure 9, Table 10) during both reading and speech processing. The blind subjects showed a greater correlation during reading between the left vOT and the occipital cortex (V1/V2) than the sighted (Figure 10, Table 11). 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.

Table 10. Functional connectivity with the left vOT in the sighted group during reading and speech processing.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Speech processing > Reading							
Lingual Gyrus, Precuneus	L	-14	-40	-2	5.40	116	0.009
Reading-related connectivity							
Middle Occipital Gyrus, Fusiform Gyrus, Inferior Parietal Lobule, Lingual Gyrus, Superior Occipital Gyrus, Superior Parietal Gyrus, Cerebellum, Inferior Temporal Gyrus, Inferior Occipital Gyrus, Middle Temporal Gyrus, Calcarine, Cuneus, Postcentral Gyrus, Precuneus, Cuneus, Angular Gyrus, Supramarginal Gyrus, Postcentral Byrus, Parahippocampal Gyrus	L/R	-38	-58	-10	41.02	30 333	< 0.001
Middle Frontal Gyrus, Inferior Frontal Gyrus (p. opercularis, triangularis), Precentral Gyrus	R	56	14	38	9.42	1729	< 0.001
Superior Frontal Gyrus, Precentral Gyrus	L	-24	-12	44	7.20	246	< 0.001
Inferior Frontal Gyrus (p. triangularis), Middle Frontal Gyrus	L	-48	48	12	6.60	376	< 0.001
Precentral Gyrus, Inferior Frontal Gyrus (p. opercularis)	L	-52	0	42	5.80	663	< 0.001
Superior Frontal Gyrus	R	30	-1	64	5.09	197	0.001
Speech processing related connectivity							
Middle Occipital Gyrus, Fusiform Gyrus, Lingual Gyrus, Superior Parietal Gyrus, Superior Occipital Gyrus, Inferior Occipital Gyrus, Cerebellum, Calcarine, Inferior Parietal Lobule, Inferior Temporal Gyrus, Middle Temporal Gyrus, Cuneus, Precuneus, Parahippocampal Gyrus, Supramarginal Gyrus, Angular Gyrus, Postcentral Gyrus	L/R	-38	-58	-10	33.20	26 673	< 0.001
Superior Frontal Gyrus, Precentral Gyrus, Middle Frontal Gyrus	L	-28	-2	52	7.80	610	< 0.001
Superior Frontal Gyrus, Middle Frontal Gyrus, Precentral Gyrus	R	32	-2	52	7.53	758	< 0.001
Inferior Frontal Gyrus (p. triangularis)	R	54	38	8	7.03	166	0.002
Inferior Frontal Gyrus (p.opercularis), Precentral Gyrus	R	44	12	28	5.95	360	< 0.001
Precentral Gyrus, Inferior Frontal Gyrus (p. opercularis)	L	-42	0	30	5.72	352	< 0.001
Anterior Orbital Gyrus	R	24	62	-16	5.34	173	0.001

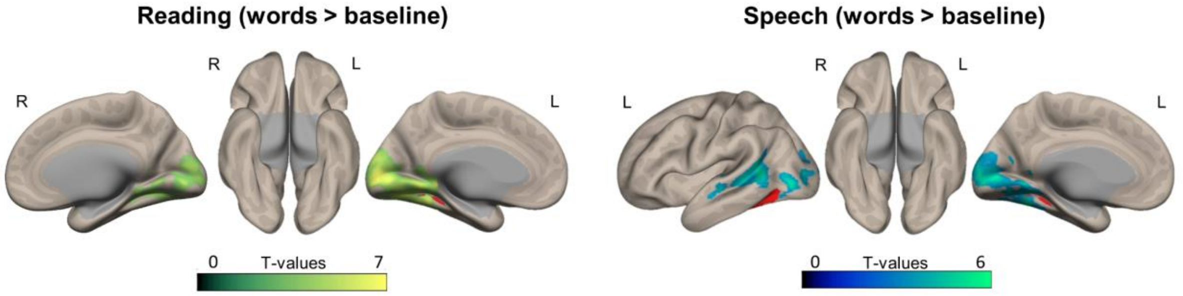

Figure 10. Regions with higher functional connectivity with the left vOT region (seed, marked in red) in the blind group than in the sighted group.

Table 11. Differences in the functional connectivity with the left vOT between the blind and the sighted groups during reading and speech processing.

Brain region	Hemisphere	x	y	z	*t*	# voxels	$p_{cluster}$ FWE
Reading-related connectivity **Blind > Sighted**							
Lingual Gyrus, Calcarine, Fusiform Gyrus, Middle Occipital Gyrus, Superior Occipital Gyrus, Cerebellum, Cuneus, Inferior Occipital Gyrus, Middle Temporal Gyrus, Hippocampus, Middle Occipital Gyrus, Precuneus, Thalamus	L/R	-36	-52	-10	7.69	8945	< 0.001
Cerebellum	R	14	-74	-26	4.75	362	< 0.001
Reading-related connectivity **Sighted > Blind**							
Superior Parietal Gyrus, Precuneus	R	24	-64	64	5.87	679	< 0.001
Middle Frontal Gyrus, Superior Frontal Gyrus	L	-32	32	32	5.36	274	0.001
Middle Frontal Gyrus	R	30	34	30	4.63	203	0.004
Speech processing related **Blind > Sighted**							
Lingual Gyrus, Calcarine, Fusiform Gyrus, Middle Occipital Gyrus, Cerebellum, Inferior Occipital Gyrus, Superior Occipital Gyrus, Cuneus	L	-36	-56	-14	6.27	3109	< 0.001
Middle Temporal Gyrus	L	-48	-36	2	5.88	1109	< 0.001
Cerebellum	R	12	-80	-24	5.23	186	0.004
Inferior Frontal Gyrus (p. traingularis, orbitalis)	L	-46	44	0	5.19	326	< 0.001
Superior Temporal Gyrus, Middle Temporal Gyrus	R	52	-40	12	5.12	439	< 0.001
Middle Temporal Gyrus	L	-64	-16	-8	5.01	244	0.001
Cerebellum	R	16	-60	-32	4.49	134	0.024
Calcarine, Superior Occipital Gyrus, Middle Occipital Gyrus	R	20	-86	10	4.30	141	0.019
Speech processing related **Sighted > Blind**							
Superior Frontal Gyrus	R	28	62	-8	5.29	275	< 0.001
Precuneus, Superior Parietal Gyrus	R	12	-64	64	4.94	308	< 0.001
Superior Frontal Gyrus	R	28	-2	52	4.71	212	0.002
Superior Frontal Gyrus	L	-22	-8	62	4.60	166	0.008

Discussion

Study 1 aimed at mapping the spoken and reading neural networks in the blind, in order to find similarities and differences in comparison to the sighted population's networks. Additionally, we wanted to test for the first time the existence of speech-reading convergence in the blind population.

As expected, we have found a significant overlap between the language networks of the blind and sighted populations. The engagement of the overlapping parts of the left vOT in Braille and print reading was confirmed (Büchel, Price, & Friston, 1998; Reich et al., 2011). The overlap between the spoken language networks of both blind and sighted in the perisylvian areas was also replicated (Bedny et al., 2011, 2015; Röder et al., 2002).

However, differences between the blind and the sighted were also found. The blind group activated the visual cortex during both reading Braille and speech processing to a larger extent than the sighted subjects. The occipital regions were activated by the blind group during speech processing, in a language-specific manner (words > non-linguistic control). The activation of the V1/V2 sites was missing in this contrast. This may be a consequence of the task choice, which was passive listening to single words. Previous studies showing engagement of early visual areas in spoken language processing in the blind used sentence-level stimuli and active tasks (Bedny et al., 2011, 2015; Lane et al., 2015; Noppeney et al., 2003; Röder et al., 2002). Another possibility is the limited size of our sample. In Study 2, where the language localizer data were analysed on an extended sample, including children, speech-specific activation of V1/V2 was found (Table 15). Language-specific activation of the occipital regions included left vOT. Speech-related activation of the left vOT in the blind has been previously reported (Bedny et al., 2011; Burton et al., 2003; Kim et al., 2017; Lane et al., 2015; Noppeney et al., 2003; Röder et al., 2002), and was interpreted as engagement in high order language processing in the blind, contrary to the low-level sensory processing in the sighted.

Additionally, in the blind, activation in the V1/V2 was reading-specific, stronger for the linguistic than non-linguistic stimuli. In the sighted subjects these regions were activated in a reading-sensitive way, with a similar level of activation for word reading and non-linguistic visual stimuli processing. This result was in line with our expectations. Previous findings also found Braille reading-related activity in the V1/V2 sites (Burton, Snyder, Conturo, et al., 2002; Gizewski et al., 2003; Sadato et al., 1996).

There were no differences in the functional connectivity of the left vOT between the reading and speech processing conditions in the blind. The left vOT was strongly connected to the language network. We consider that this indicates that the left vOT belongs to the modality independent language network in the blind.

Another difference is the fact that in the blind group, activity related to pseudowords and real words reading did not differ. Behavioural studies on Braille reading indicate that it is more sequential than print reading and employs grapho-phonological strategy independently of the lexical status of stimuli. Our results confirm these claims on the neural level. It seems that during Braille reading, the involvement of the articulatory processes is intensified, as postcentral and parietal regions, included in the dorsal language stream, were activated more by the blind than by the sighted.

Unexpectedly, a relative disengagement of the temporal cortex during Braille reading was observed. The differences between the temporal reading-related activations of the blind and the sighted group may stem from a different modality used for reading. However, we think that it is unlikely. Sighted, non-deprived subjects trained in tactile Braille reading were shown to activate the classical reading network, including the temporal cortex when reading Braille (Siuda-Krzywicka et al., 2016). In that case, the changed modality of reading did not change the organisation of the language network.

In the sighted population, MTG/STG region is connected to phonological and semantic processing (Glezer et al., 2016; Price, 2012). Multimodal integration of linguistic stimuli is also thought to take place in the temporal cortex (Hickok & Poeppel, 2007; Van Atteveldt et al., 2004). Temporal activity related to phonological processing was also shown in the blind (Arnaud et al., 2013; Burton et al., 2003), however always using auditory stimuli, never during Braille reading. On the other hand, studies looking at single Braille word reading usually failed to report extensive temporal activations similar to those observed in the sighted (Burton, Snyder, Conturo, et al., 2002; Gizewski et al., 2003; Kim et al., 2017). It is possible that the perisylvian temporal areas do not become co-opted to reading in the blind. The functions of 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.

As we observed differences in both spoken language and reading networks following visual deprivation, the speech-reading convergence regions also turned out to be different. The main regions of convergence in the blind group were bilateral vOT and this result was confirmed by all analytical approaches used. There was no overlap present in the temporal sites, in opposition to what was observed in the sighted subjects in this and previous studies (Rueckl et al., 2015). In the blind subjects, left vOT regions sensitive to reading were also significantly active for speech processing in more than 50% of our sample.

The speech-reading convergence supposedly reflects the reorganisation of the regions analysing spoken language that become co-opted for written language processing in the course of literacy acquisition (Liberman, 1992). Following this reasoning, the fact that the left vOT is the main region of speech-reading convergence in the blind would mean that it is processing speech even before Braille reading acquisition. The suggestions of the early sensitivity of the vOT to speech have been made (Bedny et al., 2015). However, they were based on a study with literate blind children as participants. So far there has been no evidence of such sensitivity in the preliterate or illiterate blind subjects.

On the other hand, the left vOT was shown to be strongly activated during Braille reading (Büchel, Price, & Friston, 1998; Sadato et al., 1996) and some evidence for selective specialisation for written language in this area was shown (Rączy et al., 2019). It is possible that due to cognitive and behavioural characteristics of Braille reading, such as the more extensive use of the sublexical route and recurrent involvement of articulatory processes, the left vOT becomes sensitive to spoken and written language following the acquisition of the sensitivity to Braille script. A recent TMS study conducted on sighted participants suggested that the vOT holds segregated neural populations selectively responding to visually and aurally presented language (Pattamadilok et al., 2019). The authors 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.

Study 2

Research questions and hypotheses

Study 2 sought to extend the results of Study 1 and examine more closely the left vOT role in linguistic processing in the blind. The left vOT turned out to be the main zone of speech-reading convergence in the blind because of its significant involvement in speech processing in this group. Additionally, the temporal regions (MTG/STG) were relatively deactivated during Braille reading. In the sighted population, these temporal sites are thought to be engaged in phonological processing during reading and speech processing (Kovelman et al., 2012) and related to the sequential, phonology-based strategy of reading used by beginning readers (Jobard et al., 2003; Martin et al., 2015). As Braille reading is more sequential than print reading, low involvement of the temporal areas in Braille reading is counter-intuitive.

As mentioned in the introduction, the precise role of the left vOT in visual reading is still debated. In the sighted, some activity in this region during speech processing was observed (Dehaene et al., 2010; Ludersdorfer et al., 2016; Planton et al., 2019; Yoncheva et al., 2010) however it is considered to be secondary to reading acquisition (Pattamadilok et al., 2019). In the blind, the activity of the left vOT during speech processing was observed more broadly (Arnaud et al., 2013; Bedny et al., 2015; Burton et al., 2003; Kim et al., 2017; Röder et al., 2002). This region was also shown to be engaged in Braille reading and it was long assumed that its function is similar to the left vOT role in the sighted population (Reich et al., 2011). However, the change in the reading modality and lack of visual inputs to the left vOT region may change its function in a significant way. It is possible that the left vOT overtakes phonological processing functions that are located in the superior temporal regions in the sighted.

The aims of Study 2 were twofold. First, we wanted to test whether the left vOT is involved in the phonological processing of spoken language in the blind and see if this involvement is different from the one observed in sighted subjects. We compared the left vOT activation to other typical language areas and the primary visual cortex to see if the pattern of activation of the left vOT is similar in these regions. The functional connectivity analyses from Study 1 indicated that left vOT is part of the modality-independent language network in the blind. Thus, we expected to find greater engagement in phonological processing in the blind than in the sighted and comparable activity of the vOT and other language network areas in this group.

It is thought that the sensitivity of the left vOT to speech in the sighted is an effect of reading acquisition and the repeated association between the spoken language and its written form

(Dehaene et al., 2010; Pattamadilok et al., 2019). Thus, the second aim of this study was to check whether the left vOT response to speech is connected to reading skills or age in the blind and the sighted. Since there were no previous studies looking at the development of the vOT sensitivity to language in the blind we treated the second research question as exploratory and we did not have specific hypotheses.

Participants

In the second study data from all participants that have undergone fMRI scanning were considered. The group included 51 blind (mean age = 23.92, *SD* = 13.98, range 6.76 – 60.32, 31 female) and 54 sighted (mean age = 22.97, *SD* = 13.45, range 6.79 – 59.83, 31 female), as four blind children had some contradictions for fMRI scanning (metallic parts in the body, abnormal brain anatomy). Forty-two participants were congenitally blind. As it was the case in Study 1, the results were recalculated excluding the early blind participants. These analyses are reported in the Appendix, as the differences between the restricted and complete samples were minor. Forty-five blind and 46 sighted participants were right-handed. Twenty-two blind subjects preferred using their left hand for reading Braille. One blind subject was excluded from all analyses due to excessive motion during scanning. Two sighted subjects were not included in the whole-brain analyses because of missing data in their individual masks. Thus, the final group sizes were: blind - 50 subjects, sighted - 52 subjects in the whole-brain analyses, and: blind - 50 subjects, sighted - 54 subjects in the ROI analyses.

fMRI tasks

Two fMRI tasks were used to answer Study's 2 research questions – a language localizer described in Study 1 and a phonological task. Only the real words and non-linguistic control conditions from the localizer task were considered in Study 2. The comparison of these two conditions is supposed to delineate language-specific activations, not connected to purely sensory perception.

The second task was the phonological task. During this task, subjects were asked to judge whether auditorily presented pairs of words rhyme or not. In the control task, subjects had to decide whether they heard the same word twice or whether the word pair consisted of two different words (Kovelman et al., 2012). The yes/no answers were given by pressing a corresponding button. Each task consisted of 20 common word pairs, presented in blocks of four pairs each. There were 10 rhyming/same pairs and 10 non-rhyming/different pairs. Both the rhyming and the control task included the same stimuli but were presented during separate runs. Words in pairs were separated by 2 seconds, and after the second word in a pair, there was a 4-second break for an answer. The functional images for this task were acquired in a whole-brain echo-planar imaging (EPI) sequence with 12 channel head coil (35 slices, slice-thickness = 3.5 mm, TR = 2000 ms, TE = 30 ms, flip angle = 90°, FOV = 224 mm^3, matrix size = 64 × 64, voxel size: 3.5 × 3.5 × 3.5 mm).

Additionally, real word reading test results were treated as a measure of reading skills level (Single Word Reading). The test is described in more detail in Study 3. Subjects were presented with lists of words of increasing length and asked to read them out loud as fast as they could. Accuracy and speed were checked. The mean number of words read correctly per minute was treated as an indicator of the reading skill.

Data Analysis

Preprocessing and whole-brain analyses

Preprocessing of the MRI data and whole-brain analyses were conducted using SPM 12 (SPM12, Wellcome Trust Centre for Neuroimaging, London, UK) running on Matlab2017b (The Math-Works Inc. Natick, MA, USA). The standard preprocessing pipeline was applied. Firstly, for all of the functional data the realignment parameters were estimated (realignment to the mean functional image), the data was slice-time corrected and resliced. The anatomical images were then coregistered to the mean functional image and segmented based on the template provided in SPM. Afterwards, the normalisation of the functional data to the MNI space was carried out with a voxel size of 2 × 2 × 2 mm. Finally, images were smoothed with an 8 mm isotropic Gaussian kernel. The ART toolbox (https://www.nitrc.org/projects/artifact_detect) was used additionally to create movement regressors as well as to detect the excessive in-scanner motion - movement over 2 mm and rotation over 0.2 mm in relation to the previous volume (default ART toolbox settings). To include a session in the analyses, 80% of the volumes needed to be artefact free. One session of one subject had to be excluded and as it was the control task run for the phonological activity analysis, this subject had to be excluded from all analyses.

Preprocessed data were analysed using a voxel-wise GLM approach. The condition blocks were convolved with the canonical haemodynamic function, and movement and motion outliers regressors were added to the model. The masking threshold in the first level model specification was defined as 0.5 to ensure good coverage of the temporal and occipitotemporal regions by the individual subjects' brain masks. One-sample *t*-tests were used to delineate regions involved in phonological processing within groups and two-sample *t*-tests to show the differences between the groups. Whole group results are reported at $p < 0.001$ voxel-level threshold with FWE $p < 0.05$ cluster-level correction.

ROI analyses

In order to test the left vOT activity during phonological processing, analyses were conducted on the data from two different types of ROI. Firstly, a literature-based ROI was used. The literature-based ROI was created as a sum of two 10 mm radius spheres around two peaks – one from the Lerma-Usabiaga et al., 2018 paper, the averaged LEX contrast peaks coordinates (-41.54, -57.67, -10.18), and the second from the Kim et al., 2017 study, the peak of activation for the auditory words > backward speech contrast averaged between the blind subjects (- 41, - 44, -17). The two spheres were intersected with the inferior temporal gyrus and fusiform gyrus masks coming from the AAL3 atlas (Rolls et al., 2020) in order to exclude voxels from the cerebellum. The ROI was created using the MarsBar toolbox (Brett et al., 2002).

Secondly, as the location of the language-sensitive voxels in the vOT can be highly variable (Saxe et al., 2006) we used an individual ROIs approach. Our goal was to study the response of the parts of the vOT that are language sensitive, independently of the modality. Thus, our ROIs were areas sensitive to reading processing and/or speech processing.

The individual ROIs were defined based on the language localizer task activation. The speech and reading words > non-linguistic control contrasts were studied, as the ones tapping into language-specific processing. The left vOT volume of the search was defined as the sum of two 20 mm radius spheres around the same peaks as the literature-based ROI, intersected with the ITG and FG masks. In order to create the individual ROIs, 50 most activated voxels (with the highest *t*-value) in the volume of search in the considered contrasts were marked. Then, the marked voxels from the two contrasts (reading and speech-processing related) were combined together to create the individual modality independent language ROI (ranging from 50 to 100 voxels with 50 voxels reflecting a complete overlap between the speech and reading-related ROIs and 100 no overlap between the speech and reading-related ROIs). The ROIs were not necessarily constructed of contiguous voxels.

In order to compare the pattern of activation of the left vOT to other parts of the language network, three additional literature-based ROIs were defined. Firstly, the primary visual cortex and Broca's region ROIs were extracted from the Anatomy Toolbox (Eickhoff et al., 2005). Additionally, left superior temporal gyrus (STG) ROI was defined based on the recent meta-analysis of the studies tapping into phonological and semantic processing (Hodgson et al.,

2021) as a 10 mm radius sphere around a peak for phonological > semantic activations in the superior temporal cortex (coordinates: -58, -23, 8).

In-house scripts written in Matlab that used SPM functions (spm_summarise for the extraction of the contrast estimates values) were used to extract ROI data. The contrast estimates for the rhyming > baseline and control > baseline contrasts from the phonological tasks were analysed. Scripts in R (version 4.04, R Core Team, 2021) were used to analyse the ROI data – compare groups and conditions, and conduct correlation analysis.

Modality-specific ROIs

It was suggested that the left vOT contains separate neuronal populations for written and spoken language processing (Pattamadilok et al., 2019). Thus, it was interesting to see if the regions found to be sensitive to different modalities are engaged in phonological processing differently. To that end, we analysed data extracted from individual, modality-dependent ROIs. The ROIs were defined as voxels sensitive either to reading or speech processing. The speech-sensitive ROIs were defined as voxels activated in the speech processing condition (words > non-linguistic control) in the localizer task and the reading-sensitive ROIs were defined as the voxels activated in the reading condition (words > non-linguistic control). It should be noted that the ROIs in the two modalities could overlap. Similarly to the modality-independent ROIs, 50 most activated voxels were selected (highest t-value).

Results

Behavioural results

Sighted subjects were able to correctly read 104.16 ($SD = 27.74$) words per minute on average, whereas blind subjects - 46.06 ($SD = 22.75$). The difference between the groups is large ($t(103) = 11.70$, $p < 0.001$) but this was expected as tactile reading is known to be slower than print reading (Veispak, Boets, & Ghesquière, 2012; Veispak, Boets, Männamaa, et al., 2012). When it comes to rhyming and control task performance, in both groups the accuracy was near ceiling level. In the rhyming task, the sighted group achieved 98.67% ($SD = 2.97\%$) accuracy on average and the blind group - 99.15% ($SD = 4.59\%$). There was a significant difference between the groups for the rhyming task accuracy, tested with the U Mann-Whitney's test ($W = 1486$, $p = 0.036$). In the control task the sighted group scored 99.43% ($SD = 1.88\%$) on average, whereas the blind group 99.15% ($SD = 2.51\%$). The analysis of reaction times (RT) indicated that the control task was significantly easier (evoked shorter reaction times) than the experimental rhyming task. This was the case for both blind (mean RT rhyming = 1.28 s, *SD* RT rhyming = 0.28 s, mean RT control = 1.16 s, *SD* RT control = 0.34 s, *W* = 1049, *p* < 0.001) and sighted (mean RT rhyming = 1.33 s, *SD* RT rhyming = 0.30 s, mean RT control = 1.13 s, *SD* RT control = 0.27 s, *W* = 1335, *p* < 0.001). The differences between the groups in reaction times were not significant for either of the tasks (rhyming *W* = 1159, *p* = 0.444; control *W* = 1323, *p* = 0.731).

Whole-brain analyses

Localizer

As the group in Study 2 was extended in comparison to Study 1, the analysis of the language localizer task activations was conducted again and is reported briefly. The regions activated by the localizer task were largely the same as in Study 1.

Reading

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 (Table 12, Figure 11). 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 (Table 12, Figure 12). The sighted subjects activated bilateral temporal cortices (STG, MTG) and bilateral occipital clusters (inferior occipital gyri) more than the blind subjects (Table 12, Figure 12).

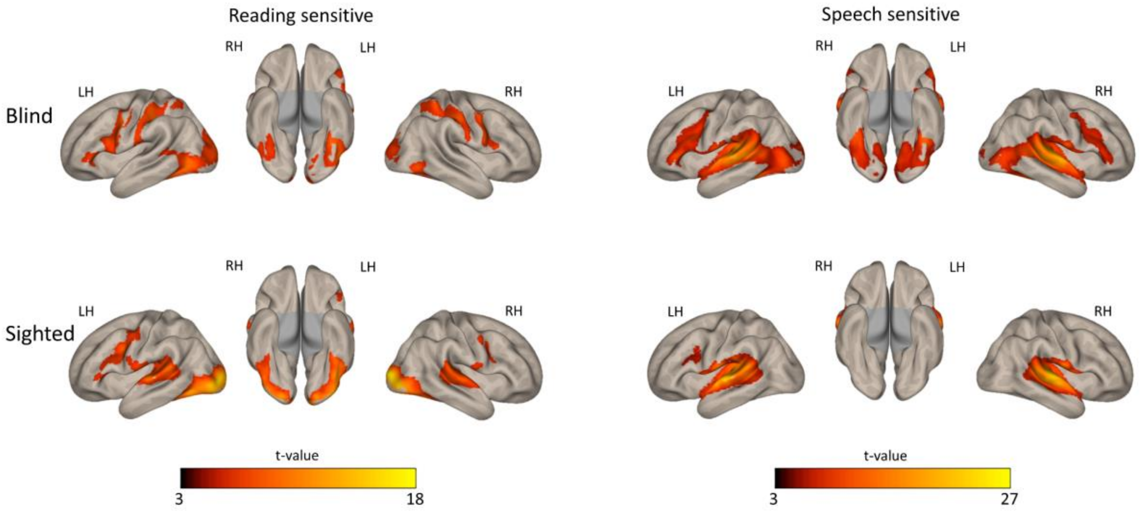

Figure 11. Group level activations for the reading- and speech-senstivie (words > baseline) contrasts from the language localizer task.

Table 12. Group-level activations and the results of the group comparison of the activations in the reading words > baseline contrast in the language localizer task.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Middle Occipital Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus, Middle Temporal, Cerebellum, Superior Occipital Gyrus. Inferior Temporal Gyrus, Calcarine, Lingual Gyrus	L	-42	-68	-6	8.2	28192
Precentral Gyrus, Inferior Frontal Gyrus (pars opercularis, triangularis, orbitalis)	L	-52	4	38	8.13	14632
Postcentral Gyrus, Inferior Parietal Lobule, Superior Parietal Lobule, Supramarginal Gyrus	R	48	-24	40	7.14	12848
Postcentral Gyrus, Inferior Parietal Lobule, Superior Parietal Lobule, Supramarginal Gyrus	L	-46	-32	44	7.28	12032
Cerebellum, Inferior Temporal Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus	R	30	-64	-24	6.84	9384
Precentral Gyrus, Inferior Frontal Gyrus (pars opercularis)	R	54	8	26	7.09	8136
Middle Occipital Gyrus, Superior Occipital Gyrus, Cuneus, Calcarine	R	30	-90	10	4.47	4936
Supplementary Motor Area	L/R	-4	-2	64	6.43	4200
Sighted						
Middle Occipital Gyrus, Inferior Occipital Gyrus, Fusiform Gyrus, Cerebellum, Inferior Temporal Gyrus, Lingual Gyrus, Calcarine, Superior Occipital Gyrus	L	-28	-92	-4	16.9	29976
Inferior Occipital Gyrus, Middle Occipital Gyrus, Inferior Temporal Gyrus, Fusiform Gyrus, Lingual Gyrus, Cerebellum, Calcarine, Cuneus, Superior Occipital Gyrus, Middle Temporal Gyrus	R	24	-96	6	17.2	23224
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Heschl Gyrus, Postcentral Gyrus	L	-62	-20	2	8.29	21360
Superior Temporal Gyrus, Middle Temporal Gyrus, Heschl Gyrus, Rolandic Operculum	R	62	-30	6	7.7	16840
Precentral Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis), Postcentral Gyrus	L	-38	2	30	6.99	11056
Precentral Gyrus, Inferior Frontal Gyrus (pars opercularis)	R	44	8	34	5.07	2504
Blind > Sighted						
Lingual Gyri, Calcarine, Cuneus, Superior Occipital Gyrus, Cerebellum, Fusiform Gyri, Middle Occipital Gyri	L/R	2	-84	14	9.69	59248
Postcentral Gyrus, Superior Parietal Lobule, Supramarginal Gyrus, Inferior Parietal Lobule	R	48	-22	38	8.26	16616
Postcentral Gyrus, Inferior Parietal Lobule, Superior Parietal Lobule, Supramarginal Gyrus	L	-50	-28	42	7.08	14088
Inferior Frontal Gyrus (pars opercularis), Precentral Gyrus	R	54	8	24	5.37	2160
Sighted > Blind						
Precuneus, Middle Cingulate, Angular Gyrus, Supplementary Motor Area, Posterior Cingulate, Middle Occipital Gyrus, Paracentral Lobule, Middle Temporal Gyrus, Cuneus, Inferior Parietal Lobule	L/R	4	-30	36	5.89	43024
Superior Temporal Gyrus, Insula, Heschl Gyrus, Rolandic Operculum, Hippocampus, Middle Temporal Gyrus	R	46	-20	8	7.3	22696
Superior Temporal Gyrus, Middle Temporal Gyrus, Insula, Heschl Gyrus, Hippocampus, Rolandic Operculum	L	-38	-32	14	7.26	21688
Middle Occipital Gyrus, Inferior Occipital Gyrus, Calcarine, Superior Occipital Gyrus, Lingual Gyrus, Fusiform Gyrus	L	-22	-92	-2	10.1	6392
Inferior Occipital Gyrus, Middle Occipital Gyrus	R	24	-90	0	8.68	6032
Angular Gyrus, Middle Occipital Gyrus	L	-34	-68	28	4.83	5720
Superior Frontal Gyrus, Middle Frontal Gyrus	R	24	14	50	4.43	2312

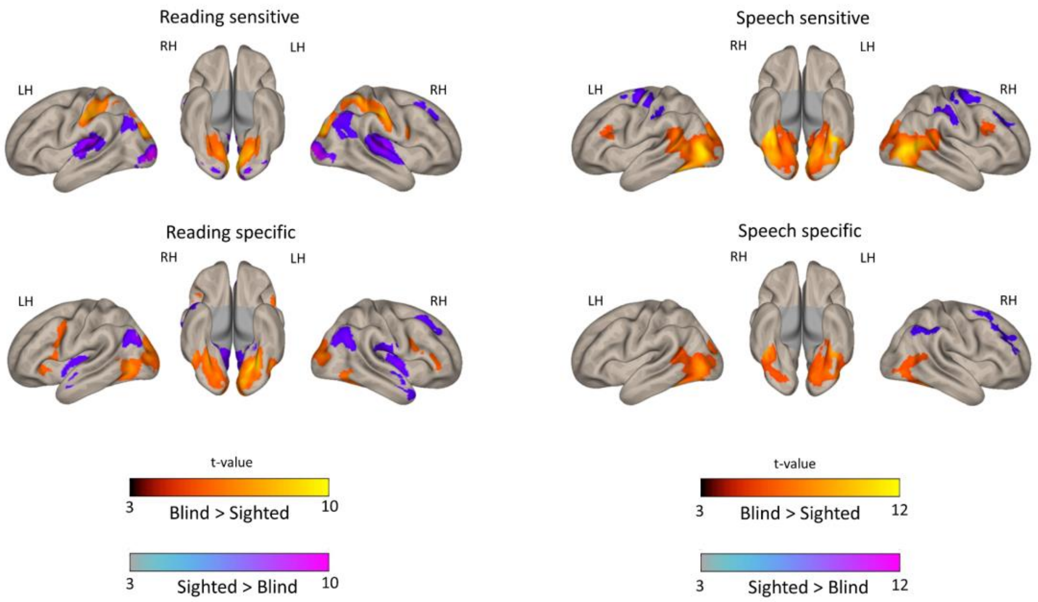

Figure 12. Group-level comparisons for the language-specific (words > control) and language-sensitive (words > baseline) contrasts from the language localizer task.

Contrast comparing reading real words to non-linguistic control stimuli (sets of “#” symbols or ⠿ Braille sign) was used to delineate regions with activation specific to reading. Both blind and sighted subjects activated left vOT during reading, as well as left precentral and postcentral gyri and some parts of the primary visual cortex (Table 13, Figure 13). In the blind group, the vOT activation was bilateral and extended to large portions of the occipital cortex. The frontal activation was also bilateral and included inferior frontal gyri. When groups were compared, the blind group was shown to activate bilateral vOT, IFG and parts of precentral gyri, as well as large portions of the occipital cortices more than the sighted group (Table 13, Figure 12). The sighted group showed more activation in the bilateral temporal cortices (MTG, STG), as well as clusters in the superior medial occipitoparietal cortex and superior frontal cortex (Table 13, Figure 12).

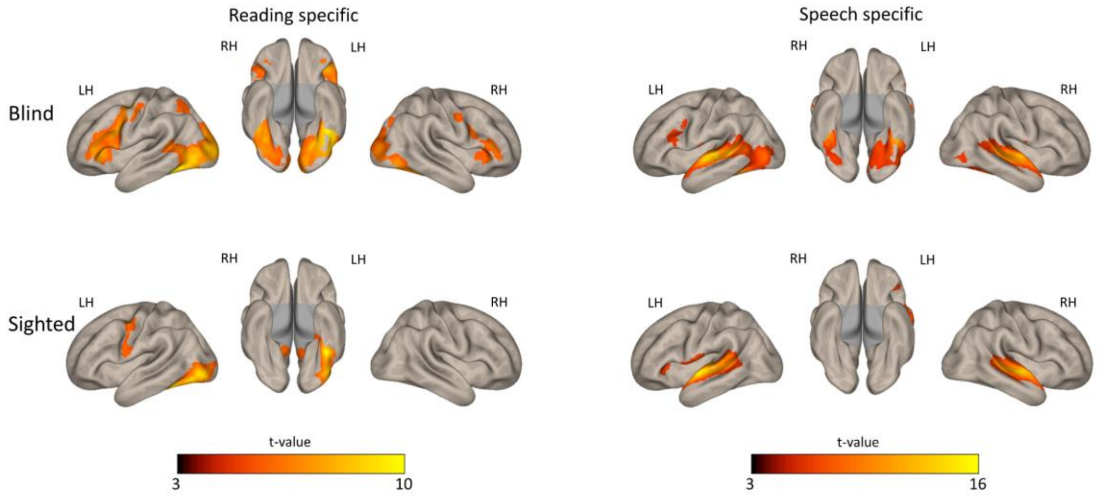

Figure 13. Group level activations for the reading and speech-specific (words > control) contrasts from the language localizer task.

Table 13. Group level activations and the results of the group comparison of the activations in the reading words > control contrast in the language localizer task.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Middle Occipital Gyri, Lingual Gyri, Calcarine, Fusiform Gyri, Middle Temporal Gyrus, Cerebelum, Inferior Occipital Gyri, Superior Occipital Gyri, Cuneus, Inferior Temporal Gyrus, Superior Parietal Gyrus	L/R	-42	-58	-14	9.90	112392
Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Precentral Gyrus, Insula, Postcentral Gyrus	L/R	-42	-4	46	6.40	36520
Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Insula, Precentral Gyrus	R	52	34	10	5.22	13664
Supplementary Motor Area	L/R	-4	2	58	6.18	9520
Sighted						
Inferior Occipital Gyrus, Fusiform Gyrus, Middle Occipital, Inferior Temporal Gyrus, Parahippocampal Gyrus, Cerebelum	L	-40	-50	-20	10.05	20368
Calcarine, Precuneus, Lingual Gyrus	L/R	16	-48	6	5.14	7592
Postcentral Gyrus, Precentral Gyrus	L	-48	-6	50	4.79	3536
Blind > Sighted						
Middle Occipital Gyri, Lingual Gyri, Fusiform Gyri, Calcarine, Cerebelum, Superior Occipital Gyri, Inferior Occipital Gyri, Middle Temporal Gyrus, Cuneus, Inferior Temporal Gyri	L/R	-26	-64	-12	8.53	74048
Precentral Gyrus, Inferior Frontal Gyrus (pars opercularis, triangularis, orbitalis), Insula	L	-36	6	22	4.98	8784
Inferior Frontal Gyrus (pars triangularis)	R	50	20	-2	4.89	3456
Inferior Frontal Gyrus (pars opercularis, triangularis), Precentral Gyrus	R	46	10	26	4.85	3128
Supplementary Motor Area	L/R	10	20	48	4.5	2576
Sighted > Blind						
Precuneus, Middle Cingulate, Calcarine, Parahippocampal Gyri, Lingual Gyrus, Posterior Cingulate, Hippocampus, Lingual Gyrus	L/R	16	-50	8	6.37	50832
Rolandic Operculum, Insula, Superior Temporal Gyrus, Heschl Gyrus, Supramarginal Gyrus, Postcentral Gyrus	R	42	-6	4	5.5	11432
Angular Gyrus, Middle Occipital Gyrus, Middle Temporal Gyrus	R	42	-74	30	4.85	5344
Anterior Cingulate, Superior Frontal Gyri	L/R	-2	44	-6	4.27	5264
Insula, Superior Temporal Gyrus, Heschl Gyrus, Middle Temporal Gyrus, Rolandic Operculum	L	-44	-8	4	5.92	4736
Middle Occipital Gyrus, Angular Gyrus	L	-40	-76	30	6.06	3792
Superior Frontal Gyrus, Middle Frontal Gyrus	R	26	16	48	4.82	3496
Middle Temporal Pole, Middle Temporal Gyrus, Superior Temporal Gyrus	R	46	16	-32	4.2	2728

Speech

In the speech-sensitive contrasts (words > baseline), the blind group, apart from the bilateral temporal regions activated also by the sighted group, activated the occipital cortex with bilateral vOT and right IFG more than the sighted group (Table 14, Figure 11). Contrast comparing listening to real words to non-linguistic control stimuli (vocoded speech) was used to delineate regions specifically activated by speech processing. Both groups activated bilateral superior regions (MTG, STG) and left IFG in response to speech (Table 15, Figure 13). Additionally, in the blind group, bilateral vOT activation was observed. Bilateral vOT was activated more by the blind group than by the sighted group (Table 15, Figure 12). The sighted subjects presented higher activation than the blind group in two right hemisphere clusters - in the frontal and parietal cortex (Table 15, Figure 12).

Table 14. Group-level activations and the results of the group comparison of the activations in the speech words > baseline contrast in the language localizer task.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Middle Temporal Gyrus, Superior Temporal Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Lingual Gyri, Calcarine, Middle Occipital Gyrus, Fusiform Gyrus, Inferior Occipital Gyrus, Superior Temporal Pole, Cuneus, Rolandic Operculus, Supramarginal Gyrus, Insula, Precentral Gyrus, Cerebellum, Heschl Gyrus, Inferior Temporal Gyrus, Superior Occipital Gyrus, Postcentral Gyrus	L/R	-56	-24	2	21.3	123128
Superior Temporal Gyrus, Middle Temporal Gyrus, Fusiform Gyrus, Superior Temporal Pole, Rolandic Operculum, Insula, Cerebellum, Inferior Occipital Gyrus, Heschl Gyrus, Inferior Temporal Gyrus, Middle Occipital Gyrus, Supramarginal Gyrus, Middle Temporal Pole	R	56	-26	4	22.3	69368
Inferior Frontal Gyrus (pars triangularis, opercularis), Precentral Gyrus	R	46	14	26	7.31	10144
Sighted						
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Superior Temporal Pole, Insula, Heschl Gyrus, Supramarginal Gyrus, Postcentral Gyrus	L	-60	-22	2	23.2	50104
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Superior Temporal Pole, Insula, Heschl Gyrus, Supramarginal Gyrus, Postcentral Gyrus	R	62	-22	6	27.4	47904
Inferior Frontal Gyrus (pars triangularis, opercularis)	L	-44	10	22	4.9	2280
Blind > Sighted						
Lingual Gyri, Middle Temporal Gyri, Middle Occipital Gyri, Calcarine, Fusiform Gyri, Cuneus, Inferior Occipital Gyri, Superior Temporal Gyri, Superior Occipital Gyri, Cerebellum, Inferior Temporal Gyri, Supramarginal Gyrus, Parahippocampal Gyrus	L/R	48	-70	0	11.3	170432
Inferior Frontal Gyrus (pars opercularis, triangularis)	R	38	12	28	4.53	2400
Inferior Frontal Gyrus (pars triangularis)	L	-44	22	24	4.43	2080
Sighted > Blind						
Supplementary Motor Area, Precentral Gyri, Postcentral Gyrus, Superior Frontal Gyri, Middle Cingulate, Inferior Parietal Lobule	L/R	-4	-6	54	6.42	30320
Postcentral Gyrus, Supramarginal Gyrus	R	44	-24	44	6.29	6408
Middle Frontal Gyrus	R	32	36	32	4.45	2752

Table 15. Group level activations and the results of the group comparison of the activations in the speech words > control contrast in the language localizer task.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Middle Temporal Gyrus, Fusiform Gyrus, Superior Temporal Gyrus, Lingual Gyrus, Middle Occipital Gyrus,Inferior Occipital Gyrus, Inferior Temporal Gyrusm, Superior Temporal Pole, Calcarine, Cerebelum	L	-60	-24	-2	15.24	47672
Superior Temporal Gyrusm, Middle Temporal Gyrus, Superior Temporal Pole, Middle Temporal Pole	R	54	-26	0	11.68	19832
Fusiform Gyrus, Inferior Occipital Gyrus, Inferior Temporal Gyrus	R	40	-44	-18	9.17	5328
Inferior Frontal Gyrus (pars triangularis)	L	-50	26	20	4.74	2920
Sighted						
Middle Temporal Gyrus, Superior Temporal Gyrus, Superior Temporal Pole, Rolandic Operculum	L	-60	-8	-4	15.23	24520
Superior Temporal Gyrus, Middle Temporal Gyrus, Superior Temporal Pole, Middle Temporal Pole	R	56	-20	-2	14.82	21200
Supplementary Motor Area	L/R	-4	2	62	5.3	2840
Inferior Frontal Gyrus (pars triangularis), Insula	L	-38	30	0	4.9	1920
Blind > Sighted						
Middle Temporal Gyrus, Fusiform Gyrus, Middle Occipital Gyrus, Lingual Gyrus, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Cerebelum, Superior Occipital Gyrus	L	-38	-50	-16	8.29	34720
Fusiform Gyrus, Middle Temporal Gyrus, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Middle Occipital Gyrus	R	40	-44	-18	7.94	11760
Sighted > Blind						
Middle Frontal Gyrus, Superior Frontal Gyrus	R	34	24	48	4.37	5920
Inferior Parietal Lobule, Angular Gyrus, Supramarginal Gyrus	R	46	-56	44	4.25	2816

Reading & Speech conjunction

Lastly, speech-reading conjunction was tested in both groups. To that end, the conjunctions of the words > baseline contrasts in reading and speech processing modalities were tested. In the sighted group, the speech-reading conjunction was observed in typical perisylvian areas (bilateral MTG, STG, left IFG). In the blind group, the conjunction was found in the bilateral vOT, as well as in the left IFG (Table 16, Figure 14).

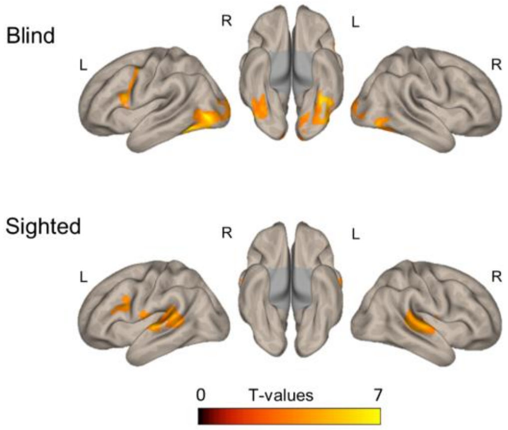

Figure 14. Speech-reading conjunction for the two groups.

Table 16. Group-level speech-reading conjunctions.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Fusiform Gyrus, Middle Occipital Gyrus, Inferior Occipital Gyrusm, Cerebelum, Lingual Gyrus, Inferior Temporal Gyrus, Middle Temporal Gyrus, Calcarine, Superior Occipital Gyrus	L	-42	-58	-12	6.77	18144
Cerebelum, Fusiform Gyrus, Inferior Temporal Gyrus, Inferior Occipital Gyrus	R	32	-64	-22	6.09	6928
Inferior Frontal (pars opercularis, triangularis), Precentral Gyrus	L	-48	12	26	5.63	3736
Sighted						
Superior Temporal Gyrus, Middle Temporal Gyrus, Rolandic Operculum, Heschl Gyrus	L	-60	-22	2	5.82	13176
Superior Temporal Gyrus, Middle Temporal Gyrus	R	52	-34	4	5.95	10136
Inferior Frontal Gyrus (pars triangularis, opercularis)	L	-42	8	24	5.04	2608

Phonological task

The phonological task (rhyming > baseline contrast) induced activation of an extensive network including perisylvian (IFG, MTG, STG), parietal and occipital regions in both blind and sighted subjects (Table 17, Figure 15). The blind group activated occipital regions, including bilateral vOT to a larger extent than the sighted group (Table 17, Figure 15). There were no regions showing stronger activation in the sighted than the blind.

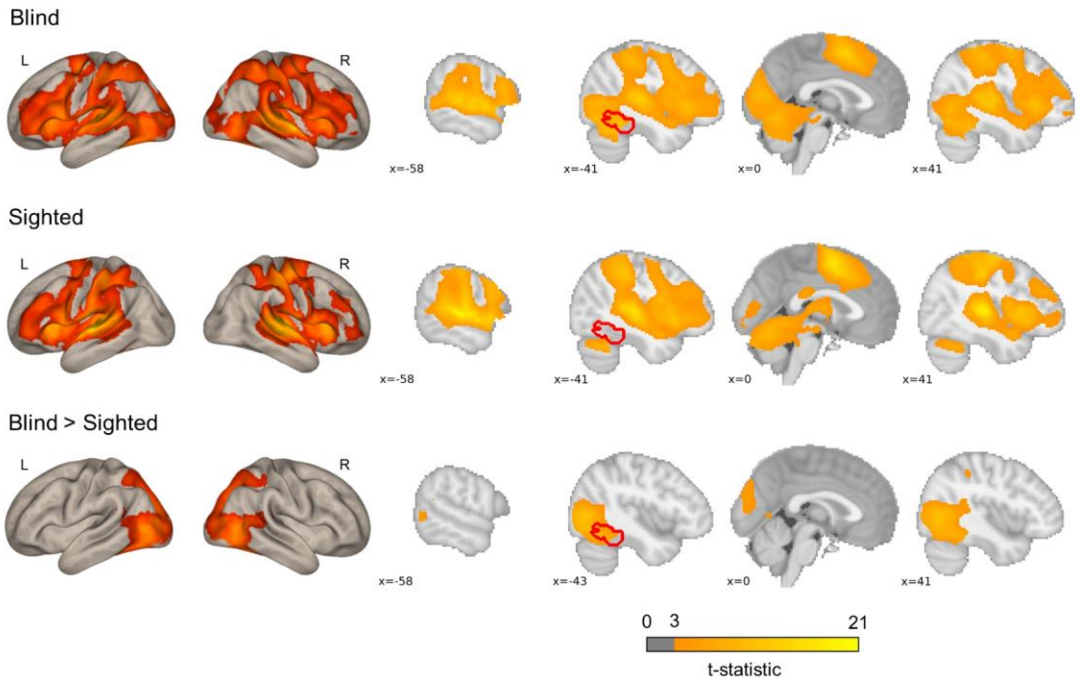

Figure 15. Rhyming task activations in the blind and sighted groups. Left vOT marked in red.

Table 17. Group level activations and the results of the group comparison of the activations in the rhyming > baseline contrast.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Superior Temporal Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Precentral Gyrus, Middle Temporal Gyrus, Postcentral Gyrus, Middle Frontal Gyrus, Supplementary Motor Area, Cerebellum, Inferior Parietal Lobule, Middle Occipital Gyrus, Lingual Gyrus, Insula, Supramarginal Gyrus, Calcarine, Fusiform Gyrus, Superior Parietal Gyrus, Rolandic Operculum, Putamen, Superior Frontal Gyrus, Cuneus, Superior Occipital Gyrus, Thalamus, Inferior Occipital Gyrus, Middle & Anterior Cingulate, Superior Temporal Pole, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Heschl Gyrus, Pallidum, Caudate, Angular Gyrus, Amygdala, Precuneus, Paracentral Lobule	R/L	62	-10	0	18.21	638928
Sighted						
Superior Temporal Gyrus, Postcentral Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Precentral Gyrus, Inferior Parietal Lobule, Middle Temporal Gyrus, Supplementary Motor Area, Middle Frontal Gyrus, Insula, Cerebellum, Rolandic Operculum, Supramarginal Gyrus, Putamen, Middle & Anterior Cingulate, Thalamus, Superior Frontal Gyrus, Caudate, Superior Temporal Pole, Superior Parietal Gyrus, Pallidum, Heschl Gyrus, Amygdala, Lingual Gyrus, Fusiform Gyrus, Hippocampus, Paracentral Lobule, Inferior Temporal Gyrus	R/L	56	-18	4	21.23	545624
Calcarine, Lingual Gyrus	R/L	-12	-72	8	5.66	7664
Blind > Sighted						
Middle Occipital Gyrus, Fusiform Gyrus, Middle Temporal Gyrus, Superior Occipital Gyrus, Cuneus, Inferior Occipital Gyrus, Lingual Gyrus, Superior Parietal Gyrus, Inferior Temporal Gyrus, Calcarine, Precuneus, Superior Temporal Gyrus, Cerebellum, Inferior Parietal Lobule, Angular Gyrus, Postcentral Gyrus	R/L	-38	-70	4	11.33	150808

In the blind, the control task (control > baseline contrast) also activated the perisylvian, parietal and occipital cortex (Table 18, Figure 16). In the sighted, the occipital activation was not present (also in the vOT). The significant differences between the groups were found in the bilateral occipital cortex (including vOT), and bilateral IFG, activated to a larger extent by the blind subjects.

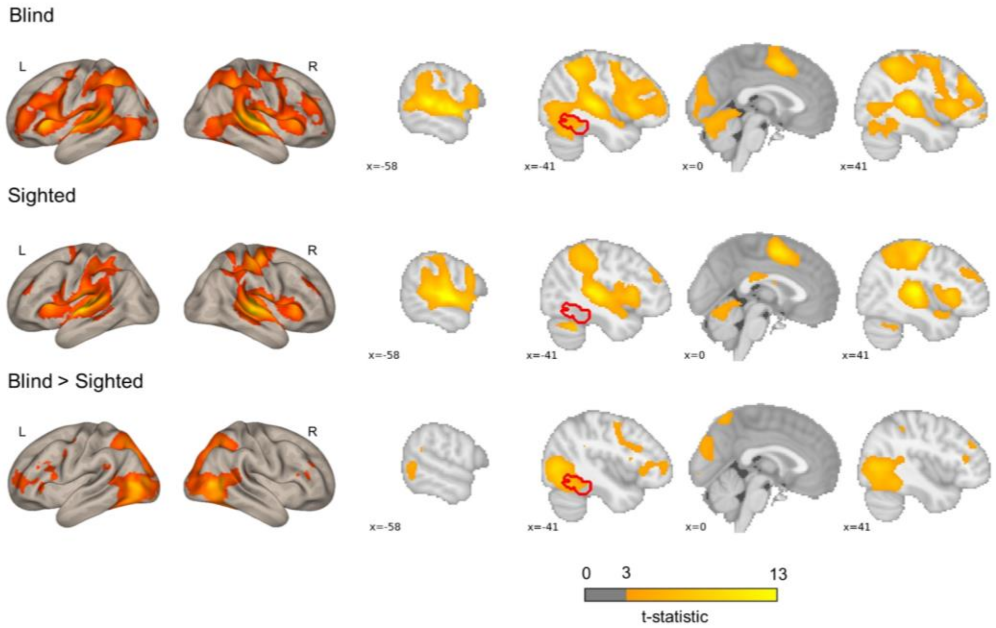

Figure 16. Group level activations and the group comparison of the activations from the control > baseline contrast, left vOT marked in red.

Table 18. Group level activations and the results of the group comparison of the activations in the control > baseline contrast.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Superior Temporal Gyri, Inferior Frontal Gyri (pars triangularis, opercularis), Inferior Parietal Lobule, Middle Temporal Gyri, Middle Frontal Gyri, Precentral Gyri, Cerebellum, Supramarginal Gyri, Insula, Supplementary Motor Area, Postcentral Gyri, Superior Parietal Gyrus, Rolandic Operculum, Middle Occipital Gyri, Calcarine, Putamen, Cuneus, Thalamu, Fusiform Gyri, Superior Frontal Gyrus, Middle Cingulate, Inferior Occipital Gyri, Superior Occipital Gyri, Inferior Temporal Gyri, Superior Temporal Pole, Heschl Gyri, Angular Gyri, Precuneus, Pallidum, Lingual Gyri, Caudate	R/L	62	-14	2	16.35	400272
Sighted						
Superior Temporal Gyri, Inferior Parietal Lobule, Postcentral Gyri, Middle Temporal Gyri, Insula, Supplementary Motor Area, Precentral Gyri, Rolandic Operculum, Supramarginal Gyri, Putamen, Inferior Frontal Gyri (pars opercularis, triangularis, orbitalis), Thalamus, Middle Cingulate, Superior Temporal Pole, Superior Frontal Gyri, Caudate, Pallidum, Superior Parietal Gyri, Heschl Gyri, Caudate, Angular Gyri, Middle Frontal Gyri, Anterior Cingulate, Middle Occipital Gyrus	R/L	58	-16	2	17.00	268864
Cerebellum	L	-24	-50	-28	11.84	18184
Cerebellum	R	28	-56	-26	7.05	5144
Middle Frontal Gyrus, Inferior Frontal Gyrus (pars triangularis), Superior Frontal Gyrus	R	36	42	26	6.23	4624
Middle Frontal Gyrus	L	-38	40	32	4.76	2912
Blind > Sighted						
Middle Occipital Gyri, Middle Temporal Gyri, Superior Occipital Gyri, Superior Parietal Gyri, Cuneus, Fusiform Gyri, Inferior Occipital Gyri, Inferior Temporal Gyri, Superior Temporal Gyri, Precuneus, Inferior Parietal Lobule, Calcarine, Lingual Gyri, Angular Gyrus, Cerebellum, Supramarginal Gyri, Rolandic Operculum, Postcentral Gyrus	R/L	50	-66	2	10.26	131920
Middle Frontal Gyrus, Inferior Frontal Gyrus (pars triangularis, orbitalis), Superior Frontal Gyrus, Insula	L	-34	52	12	4.52	8328
Precentral Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis), Middle Frontal Gyrus	L	-48	10	32	4.46	4848

Both groups activated the typical network including perisylvian regions (IFG, MTG, STG), as well as the left vOT and some parts of the primary visual cortex (Figure 17, Table 19) more during the rhyming task than during the control task. In the group comparison, a significant difference was found in the left vOT, when a more lenient statistical threshold ($p < 001$ at voxel level, cluster extent 50 voxels, as in Bedny et al., 2015) was used – the blind group activated the left vOT cluster to a larger extent than the sighted group. When cluster-level correction was used (similarly to all other comparisions), there were no significant differences between the groups for this contrast.

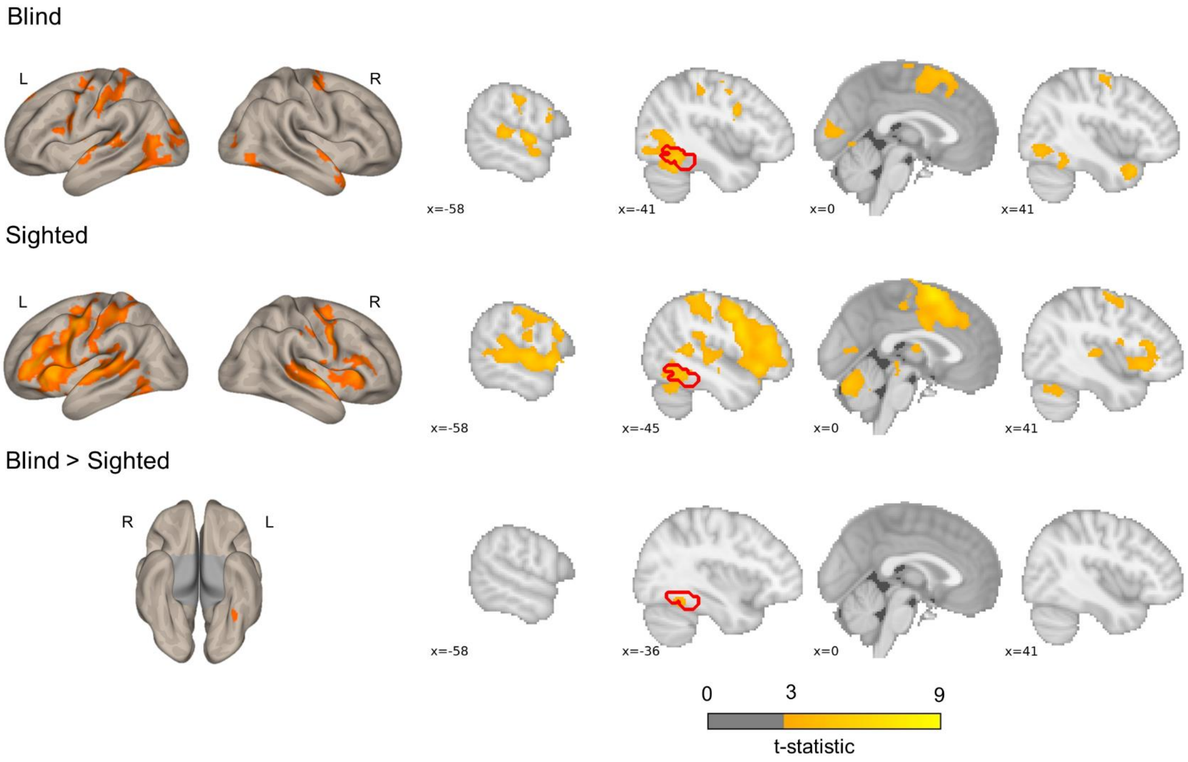

Figure 17. Group level activations and the group comparison of the activations from the rhyming > control contrast, left vOT marked in red.

Table 19. Group level activations and the results of the group comparison of the activations in the rhyming > control contrast.

	Hemisphere	x	y	z	*t*	volume mm^3
Blind						
Fusiform Gyrus, Cerebellum, Middle Occipital Gyrus, Lingual Gyrus, Calcarine, Middle Temporal Gyrus,Inferior Temporal Gyrus, Inferior Occipital Gyrus, Parahippocampal Gyrus, Cuneus, Superior Occipital Gyrus	L	-38	-54	-22	6.09	32568
Fusiform Gyrus, Cerebellum, Inferior Occipital, Lingual Gyrus, Inferior Temporal, Gyrus, Middle Occipital Gyrus, Parahippocampal Gyrus	R	36	-42	-18	5.13	10568
Supplementary Motor Area, Superior Frontal Gyrus, Middle Cingulate	R/L	-6	22	62	4.82	9152
Postcentral Gyrus, Inferior Parietal Lobule, Superior Parietal Gyrus, Supramarginal Gyrus, Precuneus_L, Precentral Gyrus	L	-54	-20	40	4.88	6848
Superior Temporal Gyrus, Middle Temporal Gyrus, Heschl Gyrus, Rolandic Operculum, Superior Temporal Pole	L	-58	-8	2	5.71	5688
Superior & Middle Temporal Pole, Superior Temporal Gyrus, Middle Temporal Gyrus, Insula	R	46	16	-28	5.93	4056
Precentral Gyrus, Superior Frontal Gyrus, Middle Frontal Gyrus	R	28	-6	70	4.54	4016
Precentral Gyrus, Superior Frontal Gyrus, Middle Frontal Gyrus	L	-30	-10	62	4.28	3336
Precentral Gyrus, Inferior Frontal Gyrus (pars opercularis, triangularis), Rolandic Operculum	L	-44	4	30	4.91	3192
Sighted						
Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Precentral Gyrus, Postcentral Gyrus, Superior Temporal Gyrus, Supplementary Motor Area, Middle Temporal Gyrus, Insula, Middle & Anterior Cingulate, Putamen, Inferior Parietal Lobule, Middle Frontal Gyrus, Superior Frontal Gyrus, Superior Temporal Pole, Superior Parietal Gyrus, Rolandic Operculum, Hippocampus, Lingual Gyrus, Supramarginal Gyrus, Pallidum, Amygdala, Heschl Gyrus, Anterior Cingulate, Parahippocampal Gyrus, Thalamus, Caudate, Cerebellum, Precuneus, Olfactory cortex, Thalamus, Fusiform Gyrus	R/L	-4	4	60	8.67	140144
Superior Temporal Gyrus, Precentral Gyrus, Inferior Frontal Gyrus (pars triangularis, opercularis, orbitalis), Insula, Superior & Middle Temporal Pole, Superior Frontal Gyrus, Postcentral Gyrus, Middle Frontal Gyrus, Heschl Gyrus, Middle Temporal Gyrus, Rolandic Opercularis, Supramarginal Gyrus, Putamen	R	62	-6	-6	6.12	41792
Cerebellum, Calcarine, Lingual Gyrus	R/L	28	-64	-26	5.92	23192
Inferior Temporal Gyrus, Cerebellum, Fusiform Gyrus, Inferior Occipital Gyrus, Middle Temporal Gyrus	L	-48	-60	-12	4.96	4768
Putamen, Caudate	R	16	10	0	5.23	4336
Blind > Sighted						
Fusiform Gyrus	L	-34	-50	-16	3.92	656
Sighted > Blind						
No suprathreshold clusters						

It was shown that in the sighted vOT activation during speech stimuli presentation is task-dependent (Yoncheva et al., 2010). Because of that, deactivation during both tasks was also analysed. In both the rhyming task (baseline > rhyming contrast) and control task (baseline > control contrast) both blind and sighted subjects showed deactivation mainly in regions that are a part of the default mode network (anterior, middle and posterior cingulate, angular gyrus, precuneus, medial frontal cortex). However, in the sighted group occipital regions were largely deactivated too. During the control task, the deactivation included bilateral vOT regions (Table 20, Figure 18).

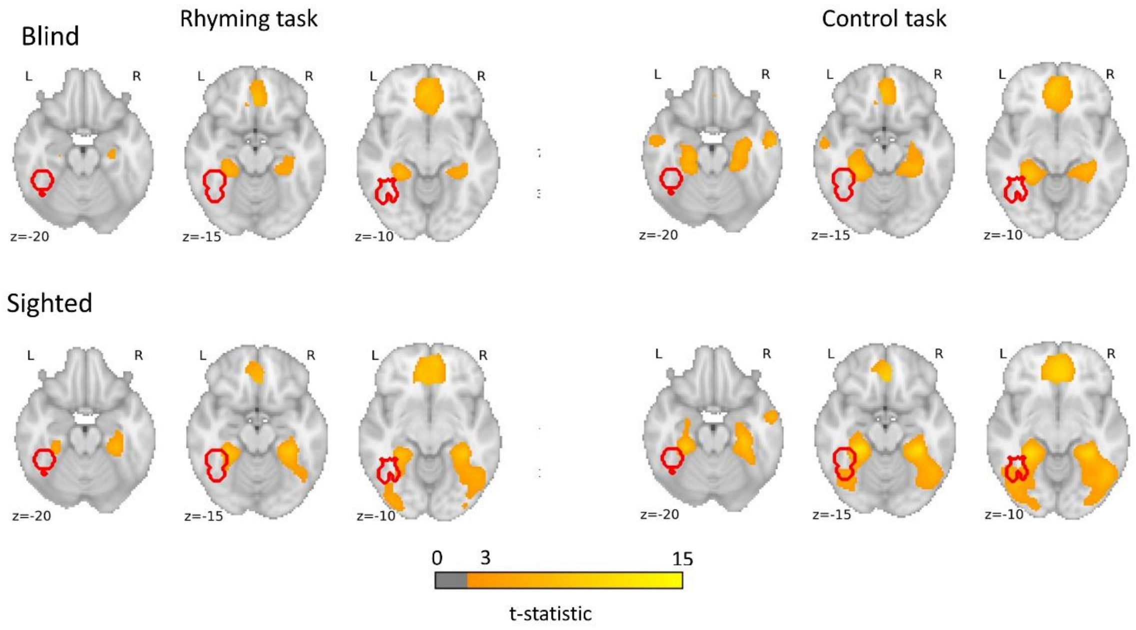

Figure 18. Deactivations in the phonological (baseline > rhyming contrast) and control (baseline > control contrast) tasks, left vOT marked in red.

Table 20. Group level deactivations in the phonological (baseline > rhyming contrast) and control task (baseline > control contrast).

	Hemisphere	x	y	z	*t*	volume mm^3
Rhyming						
Blind						
Precuneus, Middle Cingulate, Posterior Cingulate, Calcarine, Cuneus, Lingual Gyri, Hippocampus	R/L	-10	-56	18	9.91	40704
Superior Frontal Gyrus, Anterior Cingulate, Olfactory cortex	R/L	-8	44	-6	8.70	28048
Angular Gyrus, Middle Occipital Gyrus, Middle Temporal Gyrus	R	42	-74	32	11.38	9368
Angular Gyrus, Middle Occipital Gyrus, Inferior Parietal Lobule	L	-42	-72	34	11.63	8952
Superior Frontal Gyrus, Middle Frontal Gyrus	R	24	30	44	7.68	6712
Superior Frontal Gyrus, Middle Frontal Gyrus	L	-24	32	46	7.1	4760
Parahippocampal Gyrus, Hippocampus, Fusiform Gyrus	L	-30	-36	-10	6.7	3680
Parahippocampal Gyrus, Hippocampus	R	32	-36	-10	5.38	3288
Sighted						
Middle Occipital Gyri, Precuneus, Middle Temporal Gyri, Superior Occipital Gyri, Angular Gyri, Middle Cingulate, Fusiform Gyrus, Cuneus, Inferior Occipital Gyri	R/L	-42	-74	28	14.75	158592
Superior Frontal Gyri, Anterior Cingulate, Middle Frontal Gyrus	R/L	4	54	-6	10.27	43080
Superior Frontal Gyrus, Middle Frontal Gyrus	R	24	24	44	8.64	7456
Fusiform Gyrus, Parahippocampal Gyrus	L	-30	-38	-14	8.41	5008
Control						
Blind						
Precuneus, Middle & Posterior Cingulate, Parahippocampal Gyrus, Paracentral Lobule, Hippocampus Calcarine, Fusiform, Lingual Gyrus, Cuneus, Cerebellum	R/L	10	-52	16	9.38	76112
Superior Frontal Gyrus, Anterior Cingulate, Middle Frontal Gyrus	L	-4	44	-8	8.85	42984
Middle Occipital Gyrus, Angular Gyrus, Middle Temporal Gyrus	L	-40	-76	32	11.07	10904
Superior Frontal Gyrus, Middle Frontal Gyrus	R/L	26	30	46	7.79	10448
Middle Occipital Gyrus, Angular Gyrus, Middle Temporal Gyrus	R/L	44	-74	26	9.11	9680
Middle Temporal Gyrus, Middle & Superior Temporal Pole	R/L	44	14	-32	8.83	6080
Middle Temporal Gyrus, Middle Temporal Pole, Inferior Temporal Gyrus	L	-42	10	-34	5.43	3136
Sighted						
Middle Occipital Gyrus, Precuneus, Middle Occipital Gyrus, Middle Temporal Gyrus, Superior Occipital Gyrus, Fusiform Gyrus, Middle & Posterior Cingulate, Inferior Occipital Gyrus, Inferior Temporal Gyrus, Angular Gyrus, Cuneus, Parahippocampal Gyrus, Calcarine, Paracentral Lobule, Lingual Gyrus, Superior Parietal Gyrus, Postcentral Gyrus, Hippocampus, Inferior Parietal Lobule, Postcentral Gyrus	R/L	46	-72	22	13.3	206504
Superior Frontal Gyrus, Anterior Cingulate, Middle Frontal Gyrus	L	-4	38	-6	11.03	58016
Superior Frontal Gyrus, Middle Frontal	R	24	28	46	7.54	6832
Middle Temporal Gyrus, Middle Temporal Pole	R	40	18	-34	5.73	3856
Postcentral Gyrus, Precentral Gyrus	R	46	-8	34	6.38	3232
Postcentral Gyrus, Precentral Gyrus	L	-48	-10	32	5.78	2976

ROI analyses

Group and condition effects in the left vOT ROIs

Two-way mixed ANOVA was used to analyse the data from the literature-based and individual ROIs with group (Blind vs Sighted) as between-subject factor and condition (rhyming vs control task) as a within-subject factor. As the assumptions for the parametric methods (multilevel modelling ANOVA, using “lme” function from the “nlme” package, model residuals were not independent of the fitted values) were not met, a robust ANOVA method (“bwtrim” function from the “WRS2” package) was used.

When the literature-based ROI data were analysed, there was a significant main effect of group ($F(1, 45.98) = 47.47$, $p < 0.001$), as well as a significant main effect of condition ($F(1, 48.83) = 42.39$, $p < 0.001$). The interaction of group and condition did not reach significance ($F(1, 48.83) = 3.92$, $p = 0.053$, Figure 19).

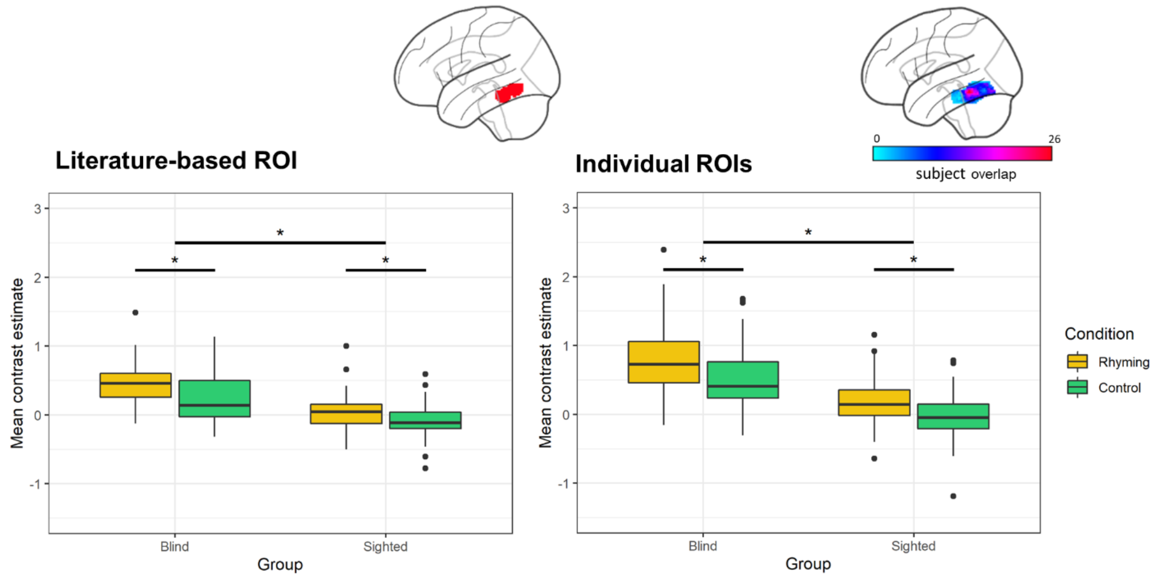

Figure 19. Contrast estimates extracted from the literature-based ROI (its location presented on the brain image) and individual ROIs (colorbar depicts the overlap of the ROIs between subjects) for the experimental conditions in both groups.

Analyses of the data from the ROIs defined individually gave similar results. There was a significant effect of group ($F(1, 46.28) = 61.16$, $p < 0.001$) and condition ($F(1, 57.94) = 41.02$, $p < 0.001$). The interaction of group and condition was insignificant ($F(1, 57.94) = 2.36$, $p = 0.130$, Figure 19).

Additionally, in order to control for the deactivation effects, the activations within the ROIs were compared to zero in every group using the non-parametric one-sample Wilcox signed-rank test. The vOT activations were significantly greater than zero for both conditions in the blind group, independently of the ROI type (literature-based ROI rhyming task mean contrast estimates = 0.45, *SD* = 0.31, *W* = 1258, *p* < 0.001, control task mean contrast estimates = 0.23, *SD* = 0.35, *W* = 1030, *p* < 0.001; individual ROIs rhyming task mean contrast estimates = 0.81, *SD* = 0.55, *W* = 1266, *p* < 0.001, control task mean contrast estimates = 0.52, *SD* = 0.47, *W* = 1234, *p* < 0.001). On the other hand, in the sighted the vOT activation was significantly greater than zero only when the rhyming task activation in the individually defined ROIs was taken into consideration (mean contrast estimates = 0.15, *SD* = 0.37, *W* = 1081, *p* = 0.007). The activity during control task was significantly below zero when the literature-based ROI data were analysed (mean contrast estimates = -0.09, *SD* = 0.24, *W* = 395, *p* = 0.006). The rhyming task-related activity in the literature-based ROI (mean contrast estimates = 0.05, *SD* = 0.26, *W* = 879, *p* = 0.242) and the control task-related activity in the individually defined ROIs (mean contrast estimates = -0.04, *SD* = 0.35, *W* = 640, *p* = 0.380) were not significantly different from zero in the sighted group. The deactivation pattern observed in the whole-brain analysis was thus largely confirmed, with the vOT activation being task dependent only in the sighted group. The blind group activated the vOT for speech processing independently of the task.

As we were interested in the relationship between left vOT activation during phonological processing and reading skills, we conducted a correlation analysis. We tested the correlation between the reading level and the mean contrast estimates from the three tasks: rhyming and control phonological tasks and the auditory non-linguistic control condition from the localizer task, to test whether the correlations were specific to language processing or rather connected in general to auditory processing. The mean contrast estimates were extracted from the literature-based and the individual vOT ROIs. The non-parametric Spearman's *rho* coefficient was used as the data distribution for the rhyming task-related contrast estimates extracted from the literature-based ROI turned out not to be normal. Bonferroni-Holm correction for the multiple comparisons was used.

The results of the analyses were independent of the ROI definition method. The correlation between reading level and activation during the rhyming was significant only in the blind subjects. All of the other correlations (with the control task and for vocoded speech processing in the blind, as well as all of the correlations in the sighted subjects) were insignificant. The exact values of the correlation coefficients are presented in Table 21.

Table 21. Correlations between the reading level or age and mean contrast estimates for rhyming, control tasks and vocoded speech processing extracted from literature-based and individual ROIs. *P*-values corrected using Bonferroni-Holm correction are presented.

			Literature ROI		Individual ROIs	
			Blind	Sighted	Blind	Sighted
words per minute	rhyming task	*rho*	**0.41**	0.28	**0.46**	0.28
		p	**0.009**	0.132	**0.003**	0.120
	control task	*rho*	0.15	0.09	0.28	0.16
		p	0.578	0.511	0.092	0.472
	vocoded speech	*rho*	0.13	-0.27	-0.02	-0.08
		p	0.353	0.094	0.916	0.524
age	rhyming task	*rho*	**0.48**	0.23	0.31	0.14
		p	**0.002**	0.178	0.081	0.933
	control task	*rho*	0.20	0.01	0.25	0.03
		p	0.156	0.961	0.152	0.855
	vocoded speech	*rho*	0.31	-0.06	0.10	-0.13
		p	0.060	1.000	0.474	0.688

As reading level was highly correlated with age (Blind: *rho* = 0.65, $p < 0.001$, Sighted: *rho* = 0.55, $p < 0.001$) it was not possible to disentangle the influence of both factors on the left vOT activation. The pattern of correlations was similar for age and reading level. None of the correlations with age w significant in the sighted group (for both literature and individual ROIs, Table 21). In the blind group, only the correlations with the rhyming task activations in the literature-based ROI were significant after the multiple comparisons correction. Partial correlations controlling for the second factor were insignificant for both age and reading level (Table 22). The only exception was the correlation with reading level controlled for age and the left vOT activation in the individual ROIs in the blind group, *rho* = 0.35, $p = 0.042$.

Table 22. Partial correlations with reading level and age in the literature-based and individual vOT ROIs. P-values corrected using Bonferroni-Holm correction presented.

		Reading level controlled for age				Age controlled for reading level			
		Literature ROI		Individual ROIs		Literature ROI		Individual ROIs	
		Blind	Sighted	Blind	Sighted	Blind	Sighted	Blind	Sighted
rhyming task	*rho*	0.16	0.18	**0.35**	0.25	0.29	0.10	0.02	-0.02
	p	0.828	0.390	**0.042**	0.225	0.088	0.910	1.000	1.000
control task	*rho*	0.03	0.10	0.16	0.18	0.14	-0.05	0.10	-0.07
	p	0.856	0.460	0.532	0.398	0.338	0.712	0.514	0.580
vocoded speech	*rho*	-0.09	-0.29	-0.11	-0.02	0.29	0.11	0.15	-0.10
	p	1.000	0.114	0.455	0.911	0.120	1.000	0.918	1.000

Modality specific individual ROIs

The voxels entering each ROI type were not necessarily independent so we were not able to conduct an ANOVA-like analysis including both the effects of group and conditions as well as ROI modality. The effect of group and condition was thus analysed using two-way robust ANOVA (“bwtrim” function) within either speech or reading-related ROI. We used a non-parametric one-sample Wilcox signed-rank test to see if the mean contrast estimates were different from zero within each group and condition, as the distributions of mean contrast estimates in the blind group were not normal (for the control task in the reading-related ROIs and both tasks in the speech-related ROIs). Spearman’s *rho* correlation coefficient was used to see if the relationship between reading level and activations in the phonological and control tasks differed between the ROIs. Results were corrected for multiple comparisons using Bonferroni-Holm correction.

In both reading and speech sensitive ROIs there was a significant main effect of group (reading: $F(1, 51.73) = 65.65$, $p < 0.001$, speech: $F(1, 44.77) = 38.38$, $p < 0.001$), and condition (reading: $F(1, 57.75) = 24.99$, $p < 0.001$, speech: $F(1, 57.99) = 53.83$, $p < 0.001$). The interaction effect was not significant in the reading-related ROIs ($F(1, 57.75) = 1.36$, $p = 0.249$) but was significant in the speech-related ROIs ($F(1, 57.99) = 4.32$, $p = 0.042$), suggesting a greater difference between the rhyming and control condition in the blind group.

For both tasks the blind group’s activations were higher than the sighted group’s activation (rhyming: reading: $W = 2350$, $p < 0.001$, speech: $W = 2147$, $p < 0.001$, control: reading: $W = 2350$, $p < 0.001$, speech: $W = 2067$, $p < 0.001$) and greater than zero (rhyming: reading: $V = 1268$, $p < 0.001$, speech: $V = 1251$, $p < 0.001$; control: reading: $V = 1227$, $p < 0.001$, speech:

$V = 1204$, $p < 0.001$). Thus, independently of ROI modality and task, the blind group activated left vOT for speech processing (Figure 20).

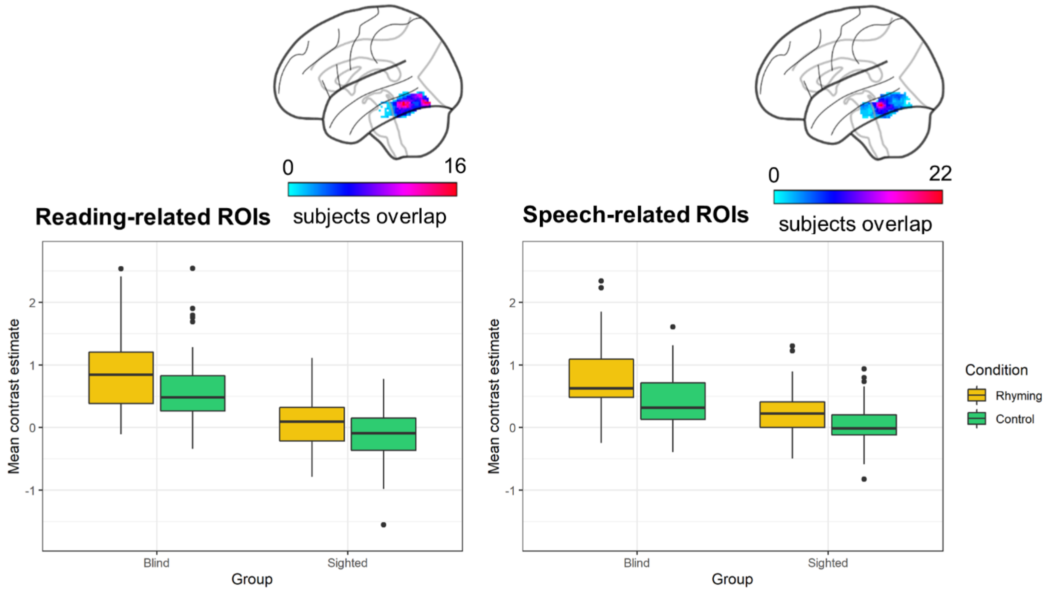

Figure 20. Contrast estimates for the reading and speech-related individual ROIs

In the sighted group the mean contrast estimates were greater than zero only when the rhyming task activations in the speech-sensitive ROIs were analysed ($V = 1182$, $p < 0.001$, Figure 20). The one-sample Wilcox signed-rank tests were insignificant when the control task contrast estimates extracted from the speech processing ROIs ($V = 837$, $p = 0.418$) were analysed, as well as the contrast estimates from the rhyming task extracted from the reading-related ROIs were tested (rhyming: $V = 918$, $p = 0.132$). When the control task activations in the reading-sensitive ROI were analysed, they turned out to be significantly lower than zero ($V = 506$, $p = 0.042$).

The correlations with reading level were only significant when the reading-related ROIs were taken into account and only in the blind group (rhyming: $rho = 0.52$, $p < 0.001$, control: $rho = 0.37$, $p = 0.017$, vocoded speech: $rho = 0.00$, $p = 0.974$). The correlations with data extracted from the speech processing ROIs were not significant in either groups (blind: rhyming: $rho = 0.27$, $p = 0.165$, control: $rho = 0.13$, $p = 0.703$, vocoded speech: $rho = 0.01$, $p = 0.924$ sighted: rhyming: $rho = 0.16$, $p = 0.751$, control: $rho = 0.00$, $p = 0.995$, vocoded speech: $rho = -0.15$ $p = 0.548$). In the sighted group, there were no significant correlations in the reading-related ROIs (rhyming: $rho = 0.30$, $p = 0.086$, control: $rho = 0.21$, $p = 0.243$,vocoded speech: $rho = -0.07$, $p = 0.604$).

Comparison to the other language-network ROIs

In order to compare the activations in the left vOT to other parts of the language network three-way mixed ANOVA was conducted with ROI (vOT vs V1 vs STG vs Broca's) and condition (rhyming vs control) as the within-subjects and group (Blind vs Sighted) as between-subjects factors. The residuals homoscedasticity assumption was not met, however, there are no robust methods for three-way ANOVA so multilevel modelling ("lme" function from "nlme" package) was used nevertheless.

There was a significant main effect of group ($\chi^2(1) = 9.44$, $p = 0.002$), ROI ($\chi^2(3) = 521.63$, $p < 0.001$) and condition ($\chi^2(1) = 30.00$, $p < 0.001$), as well as significant group by ROI interaction ($\chi^2(3) = 58.14$, $p < 0.001$, Figure 21). The condition x ROI interaction ($\chi^2(3) = 0.22$, $p = 0.974$), group by condition interaction ($\chi^2(1) = 0.00$, $p = 0.964$), as well as the three-way group by ROI by condition interaction ($\chi^2(3) = 1.39$, $p = 0.709$) were not significant. The significance of the main effect of group and ROI and the group by ROI interaction was confirmed for both rhyming and control tasks by the robust two-way ANOVA ("bwtrim" function from "WRS2" package) conducted within conditions.

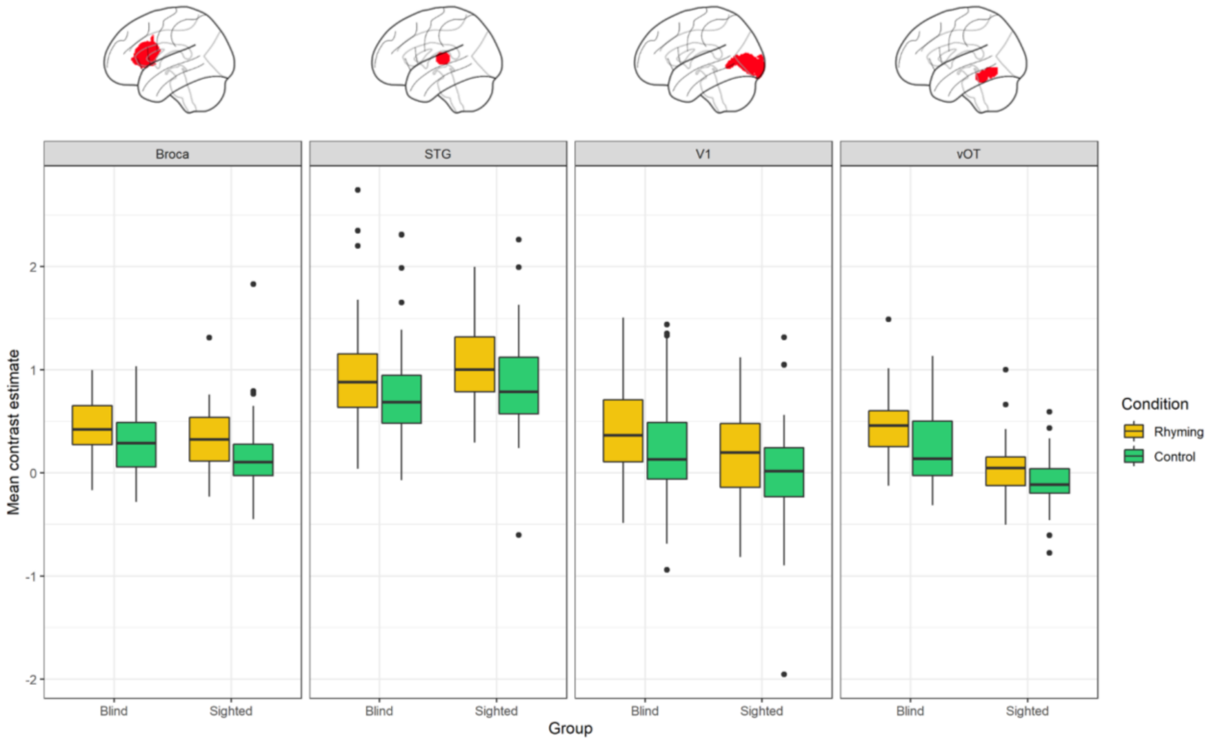

Figure 21. Contrast estimates extracted from the four language-network ROIs (their location presented on the brain images) for experimental conditions for both groups.

Pairwise comparisons were conducted using "emmeans" function (with default Tukey adjustment of p-value and $p < 0.05$ significance threshold). Post-hoc tests have shown that the activations for rhyming were higher than for control task in both groups, for every ROI (Blind: vOT: $p = 0.020$, V1: $p = 0.007$, STG: $p = 0.012$; Broca's area: $p = 0.041$, Sighted: vOT: $p = 0.020$, V1: $p = 0.007$, STG: $p = 0.012$, Broca's area: $p = 0.041$). Group by ROI interaction can be interpreted as stemming from the fact that in the occipital ROIs, for both conditions, activation was higher in the blind group than in the sighted group (Rhyming: V1: $p = 0.03$, vOT: $p < 0.001$, Control: V1: $p = 0.03$, vOT: $p < 0.001$) and the differences between the groups were not significant for the Broca's area (Rhyming: $p = 0.797$, Control $p = 0.797$) and STG ROI (Rhyming: $p = 0.999$, Control $p = 0.999$). In the blind group, for both conditions, STG ROI activation was higher than the three other ROIs (p-values of all comparisons < 0.001) and the differences between the Broca's area, V1 and vOT were insignificant. In the sighted group on the other hand, for both conditions, not only did STG ROI have higher activation than the three other ROIs (p-values of all comparisons < 0.001) but also the Broca's area had higher activation than the vOT ROI ($p < 0.001$). The differences between the vOT and V1, as well as V1 and Broca's area, were not significant.

Discussion

Study 2 aimed at testing the left vOT involvement in phonological processing in blind and sighted subjects in order to elaborate on the results of Study 1. We have found that the blind group engaged the left vOT (and V1) to a larger extent during the auditory phonological processing compared to the sighted group. The activation of the left vOT during auditory language processing may not be specific to phonology. Though we found the effect of task (phonological vs control) in the blind group, the left vOT was activated above baseline also during the control task. This was not the case in the sighted subjects where we found the left vOT deactivation during the control task, as previously shown (Ludersdorfer et al., 2016; Planton et al., 2019; Yoncheva et al., 2010). Only during the phonological task (and specifically in the neuronal populations specialised in processing spoken language), activation in the left vOT was observed in the sighted. Additionally, when four language-network ROIs were compared within the groups, vOT presented similar activation to other language-network nodes only in the blind group. In the sighted, both STG and Broca's area showed stronger activation than the vOT. Interestingly, there was no difference between the activation of V1 and Broca's area in the sighted group. These results, in line with the results of the connectivity analyses from Study 1, suggest that following visual deprivation, vOT becomes a regular node of the language network and is recruited in language processing independently of task and modality. The literature-based ROI used in the current study was quite large and spanned portions of the vOT that may have diverse functional roles (Bouhali et al., 2019; Cohen et al., 2004; Ludersdorfer et al., 2019; Pammer et al., 2004; Vinckier et al., 2007). Additionally, the significant group differences peaked anteriorly to the classical localization of print-sensitive vOT (y = -48 for rhyming > baseline, y = -50 for rhyming > control, compared to y = -57/-58 reported by Cohen et al., 2000; Lerma-Usabiaga et al., 2018). In the sighted, a gradient of specialization was observed with the more anterior parts of the vOT engaged in processing the increasingly complex stimuli with lexical content (Vinckier et al., 2007). The observed group differences may not be bound to the part of the vOT that encompasses orthographic representations in the sighted, but rather to the part of the vOT connected to the semantic system. However, the results of the literature-based ROIs and individually localized ROIs which tapped into the parts of the vOT specifically engaged in reading were the same. The observed pattern of activations was thus present in the area functionally connected to reading. Additionally, the gradient of specialization in the vOT was recently shown to be absent in blind Braille readers (Tian et al., 2022). Current results point to a changed role of the left vOT in the language system of blind individuals. The exact role of this region in linguistic processing in the blind should be a subject of further investigation.

The second goal of Study 2 was to examine the relationship between reading skills and the left vOT response to speech. In the sighted population, the left vOT is thought to be activated during spoken language processing as a result of reading acquisition (Dehaene et al., 2010; Pattamadilok et al., 2019; Planton et al., 2019) and this activation is often interpreted as the automatic activation of the orthographic codes (Ludersdorfer et al., 2016; Wang et al., 2018). Interestingly, the left vOT activations turned out to be connected to the reading level only in the blind group. In the sighted, this correlation approached significance but did not survive multiple comparisons correction. Previously such correlation was observed in young beginning readers (Wang et al., 2018, 2021) or in groups with a very broad reading skill spectrum, including illiterate subjects (Dehaene et al., 2010) or poor readers (Dębska et al., 2019). It is possible that, because the vast majority of our sighted subjects were proficient readers, we were not able to observe the significant relationship between the reading skill and the activation of the left vOT during spoken language processing. The vOT response to speech may follow the inverted U-shaped developmental trajectory, as it is the case with the vOT response to print (Chyl, Fraga-González, et al., 2021; Fraga-González et al., 2021). Thus, primary stages may be crucial for observation of the relationship between the vOT response to speech and reading skill level.

Importantly and somewhat contrary to Bedny et al. 2015 results, neither reading level nor age was correlated with activations in left vOT for non-linguistic auditory stimuli. This difference may stem from the larger age range in our compared to the previous study. Our results extend previous findings showing the left vOT involvement in speech processing in congenitally and early blind subjects (Kim et al., 2017) to other linguistic domains beyond syntax. We think that the observed differences between the blind and the sighted in the activation during a phonological task reflect a different developmental trajectory in these two groups.

Although our data do not permit testing this hypothesis directly, we think that the observed differences between the blind and the sighted in the activation during a phonological task reflect a different developmental trajectory in these two groups. The left vOT region is connected to the perisylvian language areas as well as to the occipital cortex (Yeatman et al., 2013). In the sighted population, this unique set of connections is thought to define its crucial role in reading (Dehaene et al., 2015; Saygin et al., 2016). As the left vOT is connected to both visual and linguistic areas it is a perfect candidate for a region binding the newly learned written form of language with the known spoken form. This association is so strong that the left vOT may present some sensitivity to spoken language too (Pattamadilok et al., 2019).

In individuals who are congenitally or early blind, the connections of the left vOT probably stay largely unchanged (Noppeney, 2007) however the nature of the input from the connected areas is different (Bedny, 2017). We know that the language network in the blind is very similar to the one observed in the sighted population, the difference being the inclusion of the occipital cortex (Study 1, Röder et al., 2002). The occipital cortex in the blind is thought to be involved in many high-order cognitive processes and language is one of them (Bedny et al., 2011, 2015). Thus, the left vOT, along with other occipital areas like V1, might also be incorporated into the language processing network, even before Braille reading acquisition. When blind individuals learn how to read, the left vOT becomes active during tactile reading but this activation may reflect more general linguistic processes and not solely the activation of the orthographic representations (Tian et al., 2022).

Nevertheless, we think that some specialisation for Braille reading is present in the blind subjects' vOT. It is possible that some part of the linguistically involved vOT becomes especially sensitive to Braille reading whereas the activation of the rest of the region stays connected to general language processing. This would explain why the correlation between the reading level and the activations in the left vOT was significant only when the reading-related individual ROIs were analysed. This pattern is also similar to the correlations observed in the temporal cortex of sighted beginning readers, where higher reading fluency was connected to a stronger response to spoken words in the MTG/STG region (Chyl et al., 2018). It seems that reading acquisition leads to functional refinements in the blind subjects' left vOT (in line with the interactive specialisation framework by Johnson, 2011). Such an explanation is in agreement with studies showing the left vOT specialisation for the Braille orthographic codes (Rączy et al., 2019). The exact role of the left vOT in Braille reading in the blind is yet to be discovered.

The results of Study 2 suggest that the activation of the left vOT during Braille reading in blind subjects is different in nature to the one observed in the sighted population reading print, supporting the premises of the pluripotent cortex hypothesis (Bedny, 2017). Blind subjects activated the left vOT during both speech processing conditions and independently of the ROI definition method. Contrarily, the sighted group activation for speech processing was task- (connected to the phonological task) and modality-specific (the activation was found only in the speech-specific region). We hypothesise that in the sighted the sensitivity to spoken language in the left vOT is secondary to its involvement in reading whereas in the blind the sensitivity to speech in this region comes first, although it is further refined by reading.

Study 3

Research questions and hypotheses

As it was shown in the introduction, differences in the writing systems (e.g. orthographic transparency) might to some extent affect the relationship between reading and its cognitive correlates. The influence of the modality used for reading on the cognitive correlates of reading is less studied. Meanwhile, for the majority of alphabetic languages, the construction of Braille script is completely analogical to the print alphabet. One example of such a language is Polish with uncontracted Braille, where every Braille symbol has its exact analogue in the Polish version of the Latin alphabet and the phoneme-grapheme mappings are conserved. This gives us an opportunity to study the influence of the cognitive correlates of reading in separation from other factors like orthographic transparency.

Previous, rare studies that looked for the differences between the cognitive correlates of Braille and print reading, were based on quite small samples ranging from 13 to 30 participants per group. Similarly to the sighted print reading, the correlations between PA and Braille reading and RAN and Braille reading were also found (Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013). In the blind, the PA-reading relationship was reported to be even stronger than in the sighted (Veispak et al., 2013). This stronger correlation was interpreted as stemming from the use of the grapho-phonological decoding strategy, used by the blind Braille readers independently of the stage of reading development (Veispak, Boets, & Ghesquière, 2012) as opposed to the whole-word orthographic strategy used by skilled sighted print readers. No differences were found between the level of PA or RAN skills between the two groups (Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013, though for PA see also Dodd & Conn, 2000; Greaney & Reason, 1999). The main difference related to the changed reading modality was the increase in tactile acuity in the blind compared to the sighted (Veispak, Boets, & Ghesquière, 2012; Veispak et al., 2013; Wong et al., 2011) and the fact that this perceptual ability was solely related to Braille reading. Some studies also indicate that short-term memory may be enhanced in blind subjects (Arcos et al., 2022; Bottini et al., 2016; Dormal et al., 2016; Occelli et al., 2017; Veispak et al., 2013) and that this cognitive skill is significantly related to Braille reading (Veispak et al., 2013).

The goal of Study 3 was to compare the relationship between cognitive skills and reading in a large sample of blind and sighted participants. Based on the previous studies, we expected to find a significant and independent connection between Braille reading and PA, RAN, but also tactile acuity and short-term memory. We were also interested in whether the development of reading and reading-related skills is different between the two groups. As large samples of blind participants are difficult to recruit we tackled this question with a cross-sectional approach. As no studies examined this question before we treated these analyses as exploratory.

Participants

Fifty-three blind (mean age = 23.64, *SD* = 13.74, range: 9.28 - 60.32, 30 female) and 53 sighted (mean age = 23.28, *SD* = 13.39, range: 8.97 - 59.83, 31 female) subjects were included in the experiment 3, meaning all of the participants that completed the full behavioural test battery. Two blind and one sighted participants were excluded as they were the youngest and were not administered all of the behavioural tests. Twenty-one blind participants declared no residual vision, 16 - minimal light perception, and 4 - minimal light and movement perception. Forty-four participants were congenitally blind. Forty-seven blind and 45 sighted participants were right-handed. Twenty-one of the blind participants preferred reading with their left hand.

Behavioural measures

Reading tests

Single Words Reading - the test consisted of 8 lists of six words each. The length of the words increased with every second list and varied from 2 to 11 letters. High-frequency words were used, presented in different grammatical forms (declined nouns and adjectives, infinitive or conjugated verbs, adverbs). Participants were required to read all the words aloud, as fast as possible. Blind subjects completed the task tactually and sighted subjects visually but the format of the task was analogous in both modalities. Accuracy and time were measured for each list. The outcome variable (number of words read correctly per minute) was the average of the accuracy/time ratios of all the lists.

Pseudowords Reading - the test consisted of 8 lists of six pseudowords each. The length of the pseudowords increased with every second list and varied from 2 to 11 letters. The pseudowords were derived from high-frequency real words (different from those used in the Single Word Reading test) by substituting or transposing letters or whole syllables. They were matched approximately on length, CVC structure and orthographic complexity on the real words in the Single Words Reading test. Participants were required to read all of the pseudowords aloud, as fast as possible. Blind subjects completed the task tactually and sighted subjects visually but the format of the task was analogous in both modalities. Accuracy and time were measured for each list. The outcome variable (number of pseudowords per minute) was calculated as an average of the accuracy/time ratio.

Sentence Comprehension - the test consisted of two lists of 13 short (three to five words) sentences each (e.g. “Human hand has six fingers”, “Actors play in films”). The participants were asked to read each sentence silently and say “Yes” if it was true or “No” if it was false. Blind subjects were presented with the task tactually and sighted visually. Three demonstration items were presented to the participants at the beginning of the test. The time and accuracy were measured; the outcome variable was the accuracy/time ratio.

Timed Pseudowords Reading - This task was a component of a standardised dyslexia assessment battery (*Łatysz* subtest, Bogdanowicz et al., 2008) - participants were presented with a list of pseudowords arranged in verses and were asked to read aloud as many items as possible in one minute. Blind participants were presented with the pseudowords tactually and sighted subjects - visually. The outcome variable was the number of correctly read pseudowords.

Phonological awareness tests

Phoneme Deletion - the participants were asked to pronounce a word given by the experimenter without indicated phoneme (e.g. /zdrɔvɨ/ without /d/ → /zrɔvɨ/). First, an example was presented with six training items and then the participants were presented with 26 test items. Time and accuracy were measured and the outcome variable was the accuracy/time ratio.

Spoonerisms - word pairs were presented by the experimenter and the participants were asked to exchange the first syllables of the two words (e.g. /nɔvɛ dɔmɨ/ → / dɔvɛ nɔmɨ/). Participants were presented with five training items. Afterwards, pairs of words were pronounced by the experimenter, and accuracy was measured. The test was interrupted after one minute. The outcome variable was the number of correctly spoonerised word pairs per minute.

Vowel Replacement - participants were asked to replace the vowel /a/ with /u/ in words pronounced by the experimenter. Participants were presented with three training items first and then with test items. The first 8 test items each contained only one vowel /u/ (e.g. /rak/), the other 8 contained two vowels /a/ each (e.g. /fala/). Time and accuracy were measured in both parts of the test. The outcome variable was accuracy/time ratio.

Rapid naming

Rapid Naming Letters (RAN Letters) - two test lists and one training list of single letters were presented to the participants. The training list consisted of 5 different letters, presented repeatedly in pseudorandom order in two lines, 5 letters per line and the test lists consisted of the same 5 letters, 4 lines, 6 letters per line. The participants were asked to name all of the letters as fast as possible. Time and accuracy were measured. Blind participants were presented with the letter lists tactually and letters included in the test were: a, i, g, m and t. Sighted subjects were presented with the letter lists visually and letters included in the test were: a, e, k, m, s. The letters presented to blind and sighted participants were different in order to maximise the perceptual distinctiveness of the used items in both groups. The outcome variable was the time (in seconds) used to complete the task

Rapid Naming Textures (RAN Textures) - two test boards and one training board of 5 materials with different textures were presented to the participants. The training board consisted of two lines, 5 items each and the test boards consisted of 4 lines, 6 items per line. The participants were first trained in naming the five different textures (“glass”, “cardboard”, “sponge”, “net”, “velcro”) used in the test, naming them on the training board and then asked to name all the items on the test boards, as fast as possible. Both blind and the sighted completed this task tactually. The sighted subjects were blindfolded. Time to complete the task (in seconds), as well as accuracy, were both measured, though time was the only outcome variable used in the analysis

Other measures

Perceptual Speed and Accuracy - the test consisted of 12 lines of letters “c” with some “l” letters dispersed among them. The task consisted of scanning the lines and counting the “l” letters in each line. The participants were asked to say the number of the “l” letters after scanning each line. Blind subjects were presented with the test tactually and sighted visually.
The accuracy and time (in seconds) taken to complete the task were both measured, though time was the only outcome variable used in the analysis.

Orthographic Sensitivity - the participants were presented with a list of pseudowords, each item spelled in two different ways (e.g <kówka> - <kófka>, both pronounced /kufka/). One spelling was legal, i.e. consistent with the graphotactic rules of the Polish orthography and instantiated in some real words (e.g. “kówka”) while the other spelling contained graphotactically illegal letter string (e.g. <kófka>: <-ófka> string does not occur in any Polish word). Participants were asked to judge each spelling alternative and select the “better, more Polish looking” spelling variant (they were not asked to explicitly justify their choice, i.e. articulate the relevant rule). Subjects were presented with three training pairs and then with 4 lists of 7 pseudowords pairs each. The blind subjects were presented with the items tactually and the sighted subjects -

visually. Time and accuracy were measured and the outcome variable was the mean accuracy/time ratio.

Digit Span - the digit span test from either WAIS (Brzeziński et al., 2004) or WISC (Matczak et al., 2008) test batteries were used. Both forward and backward digit span was presented to the participants and accuracy was measured. The outcome variable was the sum of correct responses on the forward and backward subtests.

Grating Orientation Test (GOT) - tactile acuity measure (Van Boven & Johnson, 1994), index fingers of both left and right hands were tested. Sighted subjects were blindfolded. The outcome variable was the sum of the tactile acuity of both fingers.

Data analysis

As for some variables there was a considerable amount of missing data, missing data imputation was conducted using the “mice” package (Buuren & Groothuis-Oudshoorn, 2011, “norm.predict” imputation method). Analyses were conducted on the dataset with imputed missing values but the analyses were checked also on the original data set retaining the missing values. If the results were different between the imputed and original datasets it is mentioned in the description of the results. The results of the analyses conducted on the original dataset can be found in the Appendix. All the analyses were performed using R, version 4.1.2 (R Core Team, 2021).

Group comparisons, analysis of the relationships between age and literacy skills, as well as the analysis of the predictors of reading level were conducted on the variables described below.

Words reading (READ_WORDS): factor scores calculated based on the PCA (using “EFA.dimensions” package O’Connor, 2022) on Single Word Reading and Sentence Comprehension tests scores (accuracy/time measure). The PCA factor explained 97% of the variance of the tests.

Pseudowords reading (READ_PSEUDOWORDS): factors scores calculated based on the PCA on Pseudowords Reading and Timed Pseudowords Reading. The PCA factor explained 97% of the variance of the tests.

Phonological awareness (PA): factor scores calculated based on the PCA on Phoneme Deletion, Spoonerisms, and Vowel Replacement. The PCA factor explained 81% of the variance of the tests.

For all these variables factor scores were calculated as recommended by Field et al., 2012 (the regression method). The PCA was done on the Spearman correlation matrices as the data diverged from the normal distribution.

Additionally, the final test scores from perceptual speed, rapid naming, grating orientation test, digit span and orthographic awareness were included in the analyses.

Reliability of the tests that had at least two subtests was measured using Cronbach’s alpha coefficient (alpha function from the “psych” package, Revelle, 2022) or Spearman-Brown formula for the split-half reliability (for the tests with exactly two subtests, custom-made function). The analyses were conducted separately within the blind and sighted groups. The results are presented in Table 23. Reliability coefficients exceeded 0.70 for all tests indicating an acceptable level of reliability.

Table 23. Reliability of the behavioural measures

	Cronbach's alfa Blind	Cronbach's alfa Sighted	Split-half correlation Blind	Split-half correlation Sighted
Single Word Reading	0.92	0.89		
Pseudoword Reading	0.90	0.91		
Sentence Comprehension	0.98	0.96	0.98	0.97
Vowel Replacement	0.80	0.83	0.94	0.92
RAN Letters	0.93	0.77	0.96	0.92
RAN Textures	0.97	0.89	0.95	0.90
Orthographic Sensitivity	0.97	0.95		

The validity of the tests was explored by correlating different measures of the same broad skill reading (single word reading, pseudowords reading, sentence comprehension, timed pseudowords reading), phonological awareness (vowel replacement, phoneme deletion, spoonerisms) and rapid naming (letters and textures). Spearman correlations were used. In both groups, the tests measuring the same skills were moderately to strongly correlated (see Table 24).

Table 24. Validity of behavioural measures.

		Single Word Reading	Pseudoword Reading	Sentence Comprehension	Vowel Replacement	Phoneme Deletion	RAN Letters
Pseudoword Reading	Blind	0.88					
	Sighted	0.74					
Sentence Comprehension	Blind	0.89	0.87				
	Sighted	0.70	0.82				
Timed Pseudowords Reading	Blind	0.88	0.88	0.89			
	Sighted	0.57	0.85	0.81			
Phoneme Deletion	Blind				0.69		
	Sighted				0.73		
Spoonerisms	Blind				0.45	0.69	
	Sighted				0.73	0.78	
RAN Textures	Blind						0.45
	Sighted						0.55

Results

Group differences

As some of the variable’s distribution diverged from normal, Mann’s-Whitney’s *U* was used to compare the groups with Bonferroni-Holm correction for multiple comparisons. Sighted subjects achieved higher scores in READ_WORDS and READ_PSEUDOWORDS, Perceptual Speed, RAN Letters and Orthographic Sensitivity. Blind participants scored higher in PA, RAN Textures, GOT and Digit Span. The exact results of the analysis are presented in Table 25.

Table 25. Group comparison with the descriptive statistics within groups.

		Mean	SD	Median	Min	Max	Skewness	Kurtosis	W	p	U	p
READ_WORDS	Blind	23.89	11.36	24.95	2.14	56.84	0.46	3.21	0.97	0.298	141.00	< 0.001
	Sighted	53.97	13.23	52.91	15.49	76.75	-0.49	3.05	0.97	0.228		
READ_PSEUDOWORDS	Blind	27.97	12.94	27.88	3.28	56.45	0.37	2.82	0.97	0.199	206.00	< 0.001
	Sighted	61.66	19.03	60.26	21.13	99.82	-0.02	2.18	0.98	0.645		
PA	Blind	6.48	3.48	6.75	-1.58	11.40	-0.35	2.26	0.96	0.057	1859.00	0.004
	Sighted	4.64	3.24	4.23	-2.19	10.57	0.26	2.30	0.96	0.115		
Perceptual Time	Blind	-43.43	30.20	-31.00	-151.00	-14.00	-1.91	6.75	0.78	0.000	234.00	< 0.001
	Sighted	-14.69	8.56	-12.00	-40.00	-1.39	-1.50	4.73	0.83	0.000		
RAN (Textures)	Blind	-76.69	47.04	-60.00	-263.00	-36.00	-2.41	8.98	0.71	0.000	2120.50	< 0.001
	Sighted	-97.80	30.75	-92.00	-199.81	-55.00	-0.92	3.75	0.92	0.001		
RAN (Letters)	Blind	-31.17	14.41	-28.00	-84.00	-14.00	-1.75	6.04	0.82	0.000	750.50	< 0.001
	Sighted	-21.87	5.72	-21.00	-38.00	-12.00	-0.75	3.28	0.95	0.024		
GOT	Blind	-3.05	1.46	-2.54	-7.26	-1.25	-1.20	3.46	0.85	0.000	2018.50	< 0.001
	Sighted	-4.30	1.64	-4.50	-7.23	-1.43	0.20	1.56	0.89	0.000		
Digit Span	Blind	15.42	4.95	15.00	6.00	27.00	0.32	2.55	0.97	0.288	1886.00	0.005
	Sighted	12.59	3.56	13.00	6.00	20.00	0.06	2.59	0.97	0.162		
Orthographic Sensitivity	Blind	0.15	0.09	0.12	0.02	0.41	0.83	3.04	0.93	0.004	226.00	< 0.001
	Sighted	0.51	0.24	0.52	0.10	0.97	0.00	1.90	0.96	0.097		

Comparison between the groups in the accuracy and speed measures

The comparisons were conducted on the original dataset (missing data were omitted). As was the case for the aggregated measures of reading efficiency, sighted subjects scored higher on both accuracy and reading speed measures for most of the tests. The results are presented in Table 26. The same was true for the orthographic sensitivity test.

Table 26. Descriptive statistics and comparisons between the groups for the reading and orthographic awareness tests.

		Mean	SD	*U*	*p*	Cohen's *d*
Single Word Reading Accuracy	Blind	96.54	7.42	1068.00	0.023	-0.29
	Sighted	98.23	3.38			
Single Words Reading Time	Blind	103.08	70.63	2626.00	< 0.001	1.40
	Sighted	31.67	13.83			
Pseudowords Reading Accuracy	Blind	88.95	13.05	1017.50	0.014	-0.44
	Sighted	93.75	8.04			
Pseudowords Reading Time	Blind	137.09	69.46	2629.00	< 0.001	1.67
	Sighted	52.29	18.37			
Sentence Comprehension Accuracy	Blind	97.86	4.34	1262.00	0.306	-0.35
	Sighted	99.06	2.12			
Sentence Comprehension Time	Blind	175.75	117.74	2593.50	< 0.001	1.39
	Sighted	53.81	37.99			
Orthographic Sensitivity Accuracy	Blind	94.85	13.74	883.50	0.003	-0.69
	Sighted	102.25	6.68			
Orthographic Sensitivity Time	Blind	234.30	149.75	2451.00	< 0.001	1.48
	Sighted	70.34	45.06			

Relationship with age

To study the development of literacy skills the correlation between age and score in the aforementioned tests was analysed. As the distribution of several variables diverged from normal, Spearman’s correlation coefficient was used. Since the scatterplots suggested a nonlinear relationship between age and literacy-related variables. Spearman correlation with the logarithm of age was conducted. The correlations were compared between the sighted and the blind using the bootstrap comparison. *P*-values from these comparisons are also presented in Table 27. None of the correlations was significantly different between the blind and the sighted.

Table 27. Spearman's correlation with the logarithm of age and literacy-related variables. The p-values of the correlation coefficients were corrected for multiple comparisons using Bonferroni-Holm correction.

	Blind		Sighted		
	rho	p	rho	p	Bootstrap *p*
READ_WORDS	0.64	<0.001	0.52	<0.001	0.453
READ_PSEUDOWORDS	0.60	<0.001	0.53	<0.001	0.617
PA	0.35	0.020	0.49	0.001	0.400
Perceptual speech	0.50	0.001	0.51	<0.001	0.922
RAN Letters	0.48	0.001	0.37	0.018	0.574
RAN Textures	0.38	0.015	0.52	<0.001	0.400
Digit Span	0.46	0.004	0.35	0.022	0.505
GOT	0.11	0.423	0.33	0.017	0.270
Orthographic Sensitivity	0.65	<0.001	0.63	<0.001	0.943

Cognitive correlates of reading across groups

The influence of group (Sighted vs Blind), PA, RAN Letters, Digit Span, GOT scores on the reading level (READ_WORDS or READ_PSEUDOWORDS) was tested using linear regression (lm function). Models explained 75% for words and 81% for pseudowords of the reading skill variability (measured with adjusted R^2). For both words and pseudowords reading, group and rapid letter naming turned out to be the significant predictors (Table 28, Table 29). In both models, there was a significant group by phonological awareness interaction that indicated that phonological awareness is a significant predictor of reading skills in the sighted but not in the blind group (Figure 22, Figure 23). Additionally, for pseudowords reading, a group by RAN Letters interaction was observed. It indicated that in the sighted rapid letter naming was a stronger predictor of pseudoword reading skills than in the blind (Figure 24).
When the original dataset was tested without imputed missing values, the results were largely the same, the only difference being the group by rapid letter naming interaction was on the trend level ($p = 0.070$) for pseudowords reading.

Table 28. The linear regression results with word reading (READ_WORDS) as the dependent variable.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**26.40**	**11.07**	**41.73**	**0.00**	**3.42**	**0.001**	**NA**
Group	**35.63**	**11.59**	**59.68**	**0.92**	**2.94**	**0.004**	**0.60**
PA	0.00	-0.94	0.94	0.00	0.00	0.999	0.07
RAN Letters	**0.56**	**0.31**	**0.82**	**0.34**	**4.37**	**< 0.001**	**0.06**
Digit Span	0.58	-0.11	1.27	0.14	1.67	0.098	0.00
GOT	-2.02	-4.34	0.31	-0.17	-1.72	0.088	0.00
Group * PA	**1.64**	**0.18**	**3.11**	**0.28**	**2.22**	**0.029**	**0.02**
Group * RAN Letters	0.04	-0.57	0.64	0.02	0.12	0.904	0.00
Group * Digit Span	-0.63	-1.87	0.61	-0.22	-1.02	0.312	0.00
Group * GOT	2.45	-0.48	5.37	0.31	1.66	0.100	0.01

R^2 adjusted = 0.75

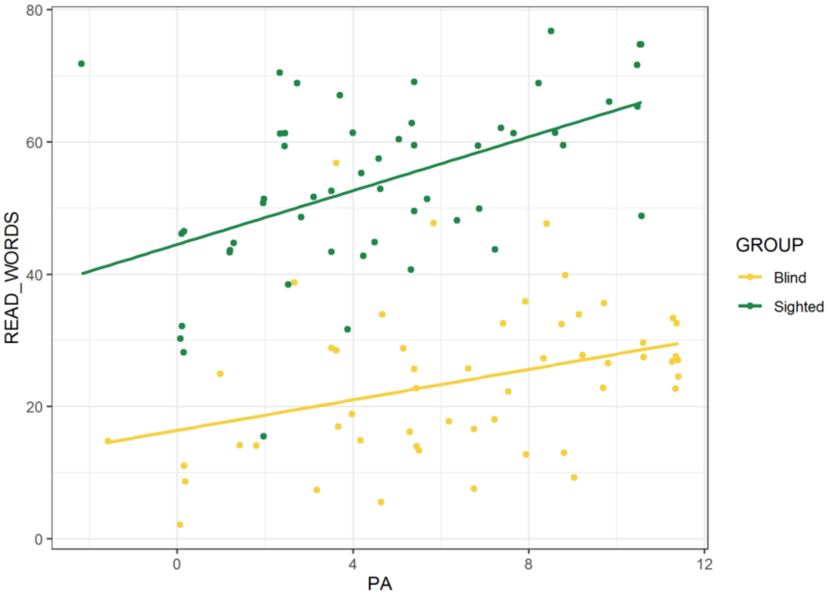

Figure 22. Group by PA interaction in the regression with READ_WORDS as the dependent variable. READ_WORDS scores are plotted as a function of PA scores with regression lines within groups.

Table 29. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**29.05**	**13.13**	**44.97**	**0.00**	**3.62**	**< 0.001**	**NA**
Group	**38.93**	**13.96**	**63.91**	**0.84**	**3.09**	**0.003**	**0.52**
PA	0.50	-0.48	1.47	0.07	1.01	0.315	0.18
RAN Letters	**0.54**	**0.27**	**0.81**	**0.27**	**4.03**	**< 0.001**	**0.05**
Digit Span	0.59	-0.12	1.31	0.11	1.64	0.104	0.01
GOT	-1.13	-3.54	1.29	-0.08	-0.93	0.357	0.00
Group * PA	**3.08**	**1.56**	**4.61**	**0.43**	**4.02**	**< 0.001**	**0.05**
Group * RAN Letters	**0.78**	**0.15**	**1.40**	**0.39**	**2.47**	**0.015**	**0.01**
Group * Digit Span	-0.52	-1.80	0.77	-0.15	-0.80	0.427	0.00
Group * GOT	-0.02	-3.06	3.02	0.00	-0.01	0.989	0.00

R^2 adjusted = 0.81

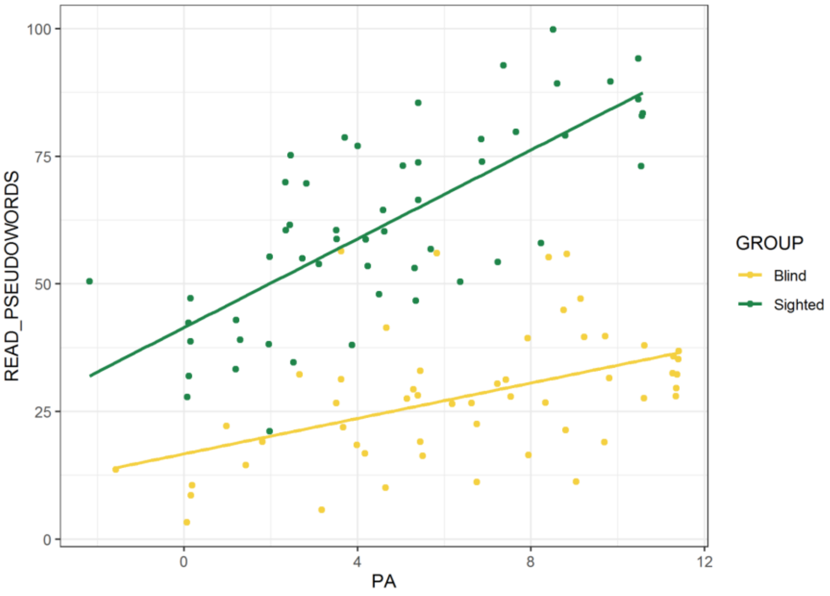

Figure 23. Group by PA interaction in the regression with READ_PSEUDOWORDS as the dependent variable. READ_WORDS scores are plotted as a function of PA scores with regression lines within groups.

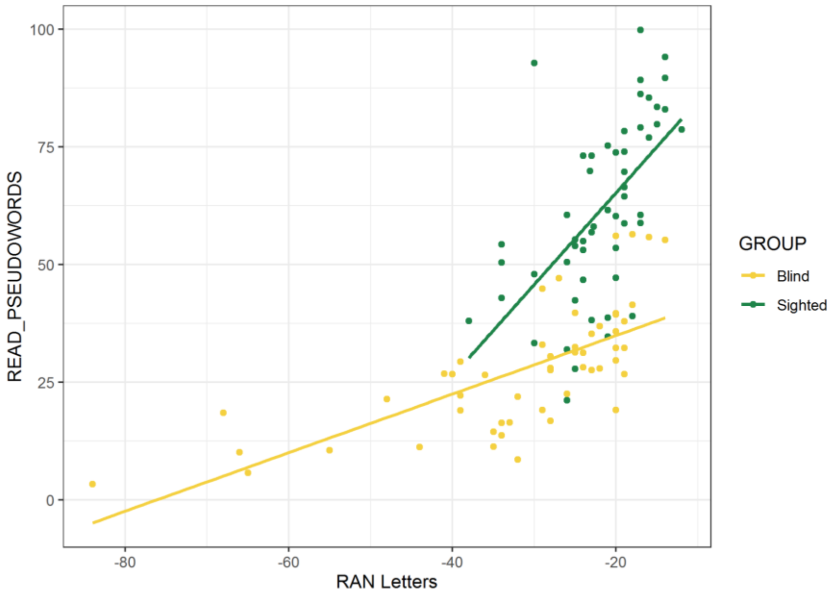

Figure 24. Group by RAN Letters interaction in the regression with READ_PSEUDOWORDS as the dependent variable. READ_WORDS scores are plotted as a function of RAN Letters scores with regression lines within groups. RAN Letters scores were reversed so that a higher score indicates better performance.

Cognitive correlates of reading within groups

First, the Spearman correlations between READ_WORDS, READ_PSEUDOWORDS, PA, RAN Letters, GOT, and Digit Span were tested. The results are presented in Table 30.

Table 30. Correlations between the literacy skills in the blind and sighted groups.

			1. READ_WORDS	2. READ_PSEUDOWORDS	3. PA	4. RAN Letters	5. Digit Span	6. GOT
1	Blind	*rho*		**0.887**	**0.368**	**0.757**	**0.555**	0.174
		p		**< 0.001**	**0.007**	**< 0.001**	**< 0.001**	0.212
	Sighted	*rho*		**0.711**	**0.492**	**0.398**	**0.331**	0.229
		p		**< 0.001**	**< 0.001**	**0.003**	**0.015**	0.1
2	Blind	*rho*			**0.509**	**0.76**	**0.59**	**0.282**
		p			**< 0.001**	**< 0.001**	**< 0.001**	**0.041**
	Sighted	*rho*			**0.735**	**0.683**	**0.523**	0.204
		p			**< 0.001**	**< 0.001**	**< 0.001**	0.143
3	Blind	*rho*				**0.359**	**0.539**	0.204
		p				**0.008**	**< 0.001**	0.144
	Sighted	*rho*				**0.466**	**0.687**	0.232
		p				**< 0.001**	**< 0.001**	0.095
4	Blind	*rho*					**0.455**	**0.495**
		p					**0.001**	**< 0.001**
	Sighted	*rho*					**0.459**	**0.331**
		p					**0.001**	**0.016**
5	Blind	*rho*						**0.272**
		p						**0.049**
	Sighted	*rho*						0.081
		p						0.562

The influence of PA, RAN Letters, Digit span and GOT on the reading level was tested within the groups using linear regressions (lm function). When word reading was the dependent variable, RAN Letters, Digit Span and GOT turned out to be significant predictors of the reading level in the blind group (Table 31, in the original dataset, working memory and tactile acuity did not reach significance as predictors, however, they explained similar proportion of variance). The model explained 51% of the word reading variance.

Table 31. The linear regression results with word reading (READ_WORDS) as the dependent variable in the blind group.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**26.40**	**13.87**	**38.92**	**0.00**	**4.24**	**< 0.001**	**NA**
PA	0.00	-0.77	0.77	0.00	0.00	0.999	0.13
RAN Letters	**0.56**	**0.36**	**0.77**	**0.72**	**5.42**	**< 0.001**	**0.35**
Digit Span	**0.58**	**0.02**	**1.14**	**0.25**	**2.07**	**0.044**	**0.04**
GOT	**-2.02**	**-3.92**	**-0.12**	**-0.26**	**-2.14**	**0.038**	**0.04**

R^2 adjusted = 0.51

Contrary, in the sighted group only phonological awareness was a significant predictor of the word reading skill (Table 32, in the original dataset also rapid letters naming was a significant predictor of words reading, here on a trend level). The model explained 26% of the word reading variability.

Table 32. The linear regression results with word reading (READ_WORDS) as the dependent variable in the Sighted group.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**62.03**	**40.23**	**83.83**	**0.00**	**5.72**	**< 0.001**	**NA**
PA	**1.64**	**0.32**	**2.97**	**0.40**	**2.49**	**0.016**	**0.25**
RAN Letters	0.60	-0.04	1.24	0.26	1.89	0.066	0.07
Digit Span	-0.06	-1.27	1.16	-0.02	-0.09	0.928	0.00
GOT	0.43	-1.66	2.52	0.05	0.42	0.680	0.00

R^2 adjusted = 0.26

When pseudowords reading was treated as the dependent variable, only RAN Letters was a significant predictor of the reading outcomes in the blind group (Table 33). 52% of pseudowords reading variance was explained.

Table 33. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable in the blind group.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**29.05**	**14.90**	**43.20**	**0.00**	**4.13**	**< 0.001**	**NA**
PA	0.50	-0.37	1.37	0.13	1.15	0.256	0.22
RAN Letters	**0.54**	**0.30**	**0.78**	**0.60**	**4.59**	**< 0.001**	**0.30**
Digit Span	0.59	-0.04	1.23	0.23	1.87	0.067	0.03
GOT	-1.13	-3.27	1.02	-0.13	-1.05	0.297	0.01

R^2 adjusted = 0.52

In the sighted group, similarly as it was the case in the model with words reading as the dependent variable, the significant reading level predictor turned out to be PA, as well as RAN Letters. The model explained 66% of the pseudowords reading variance (Table 34).

Table 34. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable in the sighted group.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**67.98**	**46.37**	**89.59**	**0.00**	**6.32**	**< 0.001**	**NA**
PA	**3.58**	**2.27**	**4.89**	**0.61**	**5.48**	**< 0.001**	**0.55**
RAN Letters	**1.32**	**0.68**	**1.95**	**0.40**	**4.17**	**< 0.001**	**0.12**
Digit Span	0.07	-1.13	1.28	0.01	0.12	0.902	0.00
GOT	-1.15	-3.22	0.93	-0.10	-1.11	0.272	0.01

R^2 adjusted = 0.66

The differences between the amount of variance explained by the group-specific models and the model including group as predictor reflect the fact that the dependent variable variance within each group was much smaller compared to variance with both groups combined. In the models including group as a predictor, it explained 75-81% of the variance. In the group-specific models, the amount of variance explained was lower, but similar to previous studies examining reading skill predictors in Polish (Dębska, Łuniewska 2021).

Discussion

Study 3 focused on the cognitive correlates of Braille reading in comparison to print reading. In line with previous studies (Carreiras & Álvarez, 1999; Mommers, 1976; Veispak, Boets, &

Ghesquière, 2012; Veispak, Boets, Männamaa, et al., 2012; Veispak et al., 2013), we found that Braille readers had much lower reading rate. This difference reflected mainly lower reading speed, which is probably the consequence of the change in reading modality. Tactile reading is, inevitably, strictly sequential, while visual reading may engage parallel processing. Tactile information is processed more slowly than visual, also demonstrated by the much faster performance of the sighted group on measures of perceptual speed and rapid naming of letters. However, when participants completed the RAN test in tactile modality, blind subjects outperformed sighted. Naming speed differences between the blind and the sighted are thus related to lower processing speed in tactile modality and not to retrieval or other cognitive elements of the RAN task.

Print readers outperformed blind readers in the orthographic sensitivity task. This difference also may have resulted from the different speeds of processing in tactile and visual modalities, however, when only accuracy was tested, the difference was still significant. The orthographic sensitivity supports the development of word-level orthographic representations (Kemény & Landerl, 2021). It is possible that as Braille reading depends heavily on the grapheme-to-phoneme conversion, the need for high-quality orthographic representations is lower. High-quality orthographic representations are crucial when the parallel processing strategy (or lexical route) is applied (Moll & Landerl, 2009). As this strategy is probably not used by Braille readers the quality of orthographic representations may be lower. On the other hand, it is possible that lower scores in the orthographic sensitivity task were also connected to the greater perceptual noise in the tactile modality. Items in one pair differed by only one letter, which may have posed greater difficulty for tactile rather than visual discrimination. Additionally, Braille readers have probably much lower print exposure than sighted print readers (Barlow–Brown & Connelly, 2002). Especially in the era of wide access to screen reading technologies, contact with the Braille script can be largely decreased after the end of formal education.

Braille readers turned out to have higher tactile acuity and stronger short-term memory skills than print readers. Such differences were reported by previous literature (Legge et al., 2008; Occelli et al., 2017; Pasqualotto et al., 2013; Veispak et al., 2013; Wong et al., 2011). Higher scores in tactile tasks in the blind are the consequences of practice in this domain connected to Braille reading (Wong et al., 2011). On the other hand, increased short-term memory performance is usually connected to increased use of the phonological loop when the visual short-term memory is inaccessible (Arcos et al., 2022). Proficiency in tactile processing and greater short-term memory explained a significant part of the variance in reading performance, only in the blind group.

Braille readers also performed better in PA tasks. Results of previous studies were mixed (sighted outperforming blind: Dodd & Conn, 2000; blind outperforming sighted: Greaney & Reason, 1999; no differences between the groups: Veispak et al., 2012, 2013) but used very diverse methodology to assess phonological skills in blind children and compare them to sighted peers. The two most recent studies: Veispak et al. 2012 and 2013 resemble the current study methodology the most and did not find any differences between the blind and the sighted on phonological awareness measures, but were performed on smaller samples.

Somewhat surprisingly the level of PA skills did not explain a significant amount of unique variance in reading efficiency in the blind group over and above tactile acuity, short-term memory and rapid naming. This result is in disagreement with the only two previous studies studying the relationship between phonological awareness and Braille reading directly, namely Veispak et al. 2012 and Veispak et al. 2013. These studies were conducted on orthographies with similar transparency (Dutch, Estonian, Schüppert et al., 2017) and in which the uncontracted Braille alphabet is also used. The weak relationship between PA tasks and reading measures in the current study did not result from a lack of variability in the blind group, as the variability measures did not differ between the groups (see Table A9 in the Appendix). On the other hand, accuracy in PA tasks was approaching ceiling level in the blind group so variability in the PA scores stemmed mostly from reaction times differences. Speed measures may have not captured individual differences connected to phonological processing but rather to other cognitive processes. Additionally, in previous studies, PA tasks were more difficult (no ceiling effect in accuracy). The PA accuracy measures correlated with reading accuracy scores in both studies (Veispak et al. 2012 and Veispak et al. 2013), whereas PA speed measures correlated with reading speed only in the Estonian population (Veispak, Boets, Männamaa, et al., 2012). The correlation between the PA and reading efficiency, taking into account both accuracy and speed were not tested. It is highly probable that in the course of development there is a strong reciprocal connection between PA and Braille reading. PA is probably a prerequisite for Braille acquisition, as it is in print reading. Previous studies were conducted on samples with a more restricted age range (9-21 years old, rather than 9-60 in the current study). It is possible that previous studies focused on a period in which both reading skills and PA skills are still developing. Braille reading, being more sequential and thus tapping more into the grapho-phonological strategy of reading may strengthen the capacity of phonological manipulations, maybe up to a point where individual differences in PA are not significantly connected with reading level. Braille readers probably never enter the whole-word reading stage, connected to successful print reading acquisition even though Braille reading becomes to some extent automatized (Krueger, 1982; Mousty & Bertelson, 1985; Simón & Huertas, 1998).

In contrast, RAN explained a unique proportion of variance of reading efficiency independently of reading modality. It is in line with the cross-linguistic studies showing a strong relationship between RAN and reading (Araújo et al., 2015; Caravolas et al., 2012, 2019; Landerl et al., 2019; Moll et al., 2014; Ziegler et al., 2010). The debate continues on the causal mechanisms linking RAN with literacy. RAN tasks, independently of the modality used to perceive the named stimuli, must involve orchestration of several cognitive sub-processes: attentional (sustained attention, response inhibition), perceptual (feature analysis, pattern recognition), lexical (phonological, semantic) and motor (articulation), and the breakdown of any of those processes may compromise both fluent naming and fluent reading (Wolf et al., 2000).

Finally, Study 3 analysed the relationship between reading and literacy-related skills and age. All of the skills have shown a logarithmic relationship with age meaning that the development plateaus at some point. No differences were found between blind and sighted participants which suggest that the differences observed in several domains do not stem from a different developmental trajectory but rather from diverse demands that a given modality imposes on the cognitive system.

General Discussion and Conclusions

The current thesis analysed the influence of visual deprivation on the organisation of the neural network processing language. We studied changes to the organisation of the spoken language network - a system that is probably evolutionary old and develops according to an innate trajectory. Our results elaborate on the limits of the changes introduced by the environmental factors to this network. Secondly, we focused on the neural network involved in reading. Contrary to speech processing, reading is a relatively recent cultural invention and the functional organisation of the brain for reading is an example of plasticity connected to learning. Studies on print reading have shown that there are biological constraints that shape the reading network making it universal between different languages and scripts. Here, we studied whether these constraints are also relevant for visually deprived brains. Despite similarities between the blind and the sighted, we have found that visual deprivation influences the reading network in an important way. Finally, we have analysed the consequences of the visual deprivation and the changed modality used for reading for the cognitive correlates of reading. Again, both similarities and differences have been found, despite analogous developmental trajectories of Braille and print reading.

Plasticity of the spoken language network

Studies presented in the thesis replicated the results showing both an overlap between the spoken language processing network of the blind and sighted populations in the perisylvian areas and the involvement of the occipital cortex in spoken language processing in the blind (Abboud & Cohen, 2019; Bedny et al., 2011, 2015; Bedny, Pascual-Leone, et al., 2012; Kanjlia et al., 2021; Lane et al., 2015; Röder et al., 2002). Regions involved in speech processing were localised in the V1/V2 loci but also in the vOT. The novelty of the current research lies in showing that occipital activity is present even during passive speech processing, without any specific linguistic task (Study 1 & 2). Moreover, our results elaborate on the vOT’s role in language processing in the blind. We have shown that following visual deprivation the vOT becomes sensitive to spoken language in a different way than in the sighted population. In the blind, the vOT is active not only during tasks that require access to orthographic representations, as is the case in the sighted (Ludersdorfer et al., 2016; Yoncheva et al., 2010). The vOT’s activation was found during solving a phonological task, as well as during passive single words processing in the blind, while the deactivation observed in the sighted group was not present in the blind. Though our sample did not permit testing this hypothesis directly, we think that our results may suggest that the development of the vOT sensitivity to language is different between the blind and the sighted. In the sighted, before reading acquisition, the left vOT is connected to perisylvian language areas, as well as to the visual cortex (Saygin et al., 2016; Yeatman et al., 2013). This connectivity makes it a perfect candidate for the region specialised in reading (Dehaene & Cohen, 2007). The increase of the sensitivity to language is a dynamic process initiated by the onset of reading acquisition (Brem et al., 2014; Dehaene-Lambertz et al., 2018). It is hypothesised that in proficient readers, the association between the written and spoken language becomes so frequent that sensitivity to speech may also emerge in the vOT (Pattamadilok et al., 2019). We hypothesise that in early blind individuals the order is reversed. Such an interpretation of the discussed results is in line with the pluripotent cortex hypothesis of cross-modal plasticity (Bedny, 2017). As presented in the introduction, the pluripotent cortex hypothesis assumes that at birth the human cortex is pluripotent with only predispositions for certain computations. What constrains the development of specialisation of a region for a given task or stimuli type is its connectivity with other, more specialised areas and consequently, the type of input it receives. So far, there are no studies that show the emergence of new connections between the vOT and other brain areas (Noppeney, 2007). The blinds' vOT is thus connected to the frontotemporal language network and occipital cortex. As no visual input accesses the vOT, the connections with the language network seem to be strengthened (Bauer et al., 2017). It is thus possible that, in the blind, even before reading acquisition the vOT receives linguistic input and becomes sensitive to speech stimuli (as suggested by Bedny et al., 2015). The sensitivity to Braille reading in this region would in this case be secondary to the vOT's involvement in spoken language processing. The speech-reading convergence observed in Study 1 would be the effect of this changed development and a consequence of the same mechanism assumed to be at work in the sighted population - engagement of the spoken language areas in the analysis of language in a new modality.

Plasticity of the reading network

We found changes not only in the spoken language network but also in the reading circuit. As expected, the occipital cortex, including early visual areas, was engaged specifically in reading (more than tactile processing of non-linguistic stimuli). Moreover, as mentioned above the speech-reading convergence was studied in the current thesis, for the first time in the blind population. It was found that the convergence was present in the blind, however, in the regions different from the typical areas of speech-reading overlap in the sighted. In the sighted, speech-reading convergence is thought to emerge as an effect of recruiting the existing neural network processing spoken language, to linguistic processing in a different modality (Liberman, 1992; Rueckl et al., 2015). Thus, perisylvian language regions, located in the superior and middle temporal gyri, as well as left inferior frontal regions are the sites of convergence. We have found that in the blind it is the vOT that is the main region of the speech-reading convergence. This is probably not only the effect of the recruitment of the vOT in the spoken language processing in the visually deprived population but also the fact that the temporal regions seem relatively disengaged during Braille reading.

This result is counterintuitive, as Braille reading is thought to rely more heavily on the grapho-phonological strategy than skilled visual reading (Veispak et al., 2012, Study 3). On the neural level, this characteristic of Braille reading seems to be confirmed by the greater involvement of the articulation-related regions for both word and pseudoword reading (Study 1) but not by the greater engagement of the superior temporal cortex. In the sighted, the activation of the superior temporal regions is thought to be connected to phonological representations (Hodgson et al., 2021). Interestingly, Study 2 has shown, confirming previously reported results (Arnaud et al., 2013; Burton et al., 2003), that these regions are still involved in the phonological processing of the spoken stimuli in the blind. However, they do not seem to be activated during reading. Our hypothesis, tested in Study 2, was that other regions take over the phonological functions of the MTG/STG regions during Braille reading in the blind. As the vOT was shown to be activated during speech processing, we tested its involvement in phonological processing. The results of Study 2 show however, that vOT's activation in the blind is not specific to phonology. Though the phonological task evoked a larger response of the vOT than the control task, the activation related to the control task was still significant.

Another explanation may be connected to the fact that, as shown in Study 3, blind subjects presented a higher level of phonological awareness skills than sighted subjects. The activity patterns of highly automatized tasks tend to resemble the inverted U-shape (Price & Devlin, 2011). Before the acquisition of specialisation of a brain region, the activity during a given task is low. It increases with the development of the skill to peak when the skill is fully learned. Afterwards, the automatisation begins which causes the activation connected to the learned task to decrease. In print reading, such a developmental trajectory was shown for the vOT region (Chyl, Fraga-González, et al., 2021; Fraga-González et al., 2021), as well as for the superior temporal region involved in the letter-speech sound integration (Romanovska et al., 2022). The disengagement of the temporal regions may reflect the greater automatisation of the phonological processing in the blind.

Yet, another possibility is that our initial hypothesis, about the vOT overtaking some of the functions fulfilled by the MTG/STG region in the sighted, was true but we were mistaken about the nature of the intercepted functions. Middle and superior temporal areas are not only involved in phonology but also in semantic processing (Hodgson et al., 2021) and multimodal integration of letters and speech sounds (Plewko et al., 2018; Van Atteveldt et al., 2004). Testing these hypotheses was outside the scope of the current thesis and therefore further research is needed.

The left vOT was not only the main region of speech-reading convergence in the blind but also the region of overlap between the neural reading networks of the blind and the sighted groups. This result replicated the previous observations on the similar engagement of this brain region in reading, independently of the modality used for reading (Rączy et al., 2019; Reich et al., 2011). Nevertheless, we think that our results indicate that the function of the vOT is different between the blind and the sighted in line with Kim et al., 2017 and Tian et al., 2022. Close proximity of the activations related to reading visually and tactually may be coincidental and not related to the computational properties of reading, as the Task Selective Sensory Independent hypothesis would predict (Amedi et al., 2017). This interpretation of current results is not in line with reports showing the specialisation of the vOT to orthographic processing in the blind (Rączy et al., 2019). However, the study that demonstrated the specialisation of the vOT for orthographic processing defined the vOT ROIs in a very specific way - as regions responsive to Braille letter strings more than to the non-linguistic Braille stimuli (the six dot sign - ⠿). It is possible that in the blind, reading acquisition leads to the emergence of modality-specialised regions in the vOT of the blind, some sensitive to tactile stimuli and others conserving their sensitivity to speech. The differential pattern of correlations with the reading level within the reading- and speech-related individual ROIs (Study 2) and the fact that the reading and speech-related activations did not overlap completely in the blind (Study 1) would be an argument for this interpretation. Thus, the previous study would tap only into the reading-sensitive part of the vOT. The speech-sensitive part might have shown a different pattern of specialisation. The functional organisation of the vOT in the blind, as well as the exact function of this region in the visually deprived population, requires further research.

Changes to the behavioural characteristics of reading

Visual deprivation influences not only the neural network employed for Braille reading but also the behavioural characteristics of this process. Study 3 confirmed previous small sample studies' results, showing that tactile reading is slower and more prone to errors than visual print reading (Veispak et al., 2013). This is probably due to the seriality of processing enforced by the change of the modality used for reading. Visual processing of print with practice becomes holistic and parallel (Altani et al., 2018). Tactile Braille reading, on the other hand, though automatized to some extent, as shown by the greater efficiency of reading real words in comparison to unknown pseudowords (Veispak, Boets, & Ghesquière, 2012; Veispak, Boets, Männamaa, et al., 2012), remains sequential and thus slower.

Other than that, we did not find proof of changed developmental trajectories of literacy skills. There were no differences between the correlations of studied skills with age. This suggests that the observed changes between the blind and sighted readers were the effect of learning and different cognitive demands posed on the process of reading by the changed modality. The development was not hindered because of visual deprivation. However, different domains were developed more stronlgy in the blind than in the sighted. This was reflected in the discovered group differences. Blind subjects performed better in verbal short-term memory, PA and tactile acuity tasks. Sighted subjects were more skilled when it comes to reading efficiency, rapid naming of letters, perceptual speed and orthographic sensitivity.

What domains are more important for Braille than print reading was demonstrated by the analysis of the cognitive correlates of reading in both modalities. Rapid naming turned out to be a universal correlate of reading, independently of the modality used for reading. This result strengthens the interpretation of the RAN skills as very general, combining many different cognitive processes. However, it was confirmed, in line with Veispak et al., 2012, 2013, that tactile and memory factors become more important when literacy is tactile and not visual. Another difference was the relationship with phonological awareness in the two groups. In line with the existing literature on the cognitive correlates of reading in the sighted, PA turned out to be one of the most important predictors for the reading level in the sighted group, especially important for phonologically more demanding, pseudowords reading. In the blind, this was not the case. PA was correlated with the reading scores however, did not explain a significant portion of variance when other factors were taken into account. Moreover, the blind subjects scored higher in the PA tasks. Such results may be an effect of reciprocal processes between PA and reading. We think that PA is a prerequisite for reading acquisition but the extensive and prolonged (in comparison to print reading) use of the grapho-phonological strategy in Braille strengthens the PA skills. It is possible that the large age range in our sample prevented us from observing the significant influence of PA on the reading scores, as the majority of our sample were skilled Braille readers. It is also possible that our task was not appropriate for studying the blind population with enhanced phonological abilities. The accuracy of the blind participants was on a ceiling level and thus maybe an important part of the variance in the blind participants' performance in PA was not captured making it impossible to observe the PA relationship with reading skills.

Conclusions

Research presented in the current thesis demonstrated that the context of the developmental processes is as important as innate mechanisms that are at the stem of these processes. We think that the pluripotency of the cortex and the dependence of the regions' functional role on their connectivity with different networks are the guiding principles in the development of the functional organisation of the human brain. However, linguistic processing conserves some universal traits, independently of experience. These universals are probably connected to the fact that these linguistic processes always serve the same goal - communication and sharing of knowledge.

Limitations

The research presented in this thesis was not without limitations. First of all the sample size, though comparable to most of the imaging studies on blind participants, may have been insufficient. The recommended sample size for fMRI studies looking for medium to large effects (Geuter et al., 2018), as well as reliably estimating the correlations between behavioural outcomes and brain activity (Grady et al., 2021) is about 80 participants. Much larger samples are also needed to reliably detect differences between the correlations in two groups[1]. The current sample was of convenience - all of the participants that provided informed consent to the study were enrolled. Data from special groups, like blind participants, are quite difficult to acquire. Despite considerable effort, the achieved sample size may not be sufficient to assure the reliability of the observed effects.

Another problem in the currently presented research was the age range of the studied group. On the one hand, it may have been too restricted because it did not include subjects at the beginning stages of reading acquisition and prereaders. This was especially problematic for the analyses of the sighted sample. As mentioned in the discussion of Study 2, not including participants at the early stages of reading acquisition might have prevented us from seeing the correlation between the left vOT activity during phonological processing and the reading level. The inclusion of a group of blind prereaders would also enable testing the hypothesis of the vOT engagement in speech processing prior to Braille reading acquisition. Such a group is again extremely difficult to recruit (e.g. in the school year 2017/2018 only three blind children without disabilities other than blindness were attending first grade in Laski primary school for visually impaired children).

On the other hand, the age range in the current research was relatively large. Matching the difficulty levels of behavioural tasks applied to a group with such age differences (from 6 to 60) is very demanding. The tests that were possible to be completed by younger children may have been too easy for more skilled, adult participants. For that reason, it is possible that we missed some important developmental characteristics of Braille reading.

The choice of the task used in the fMRI studies was not ideal either. In Study 1 a passive language localizer was chosen. The goal was to image the language network that would not be specifically connected to any particular language task (as in Chyl et al., 2018 and Malins et al., 2016). However, there are a number of problems with the use of a passive task. Firstly, we

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[1] https://garstats.wordpress.com/2019/06/17/compindcorr/

were not able to control whether the subjects paid attention to all of the stimuli. Secondly, the task may have been more engaging for the blind participants than for the sighted. As presented in Study 3, Braille reading is slower and more sequential than print reading. Our fMRI setting required managing the Braille displayer by the blind participants. Sighted subjects could simply look at the screen. The stimuli used in the experiment were high-frequency, short words. Such stimuli were read by the sighted participants quite automatically. This may have caused less extensive activation in the reading network of sighted participants, compared to the blind. The inclusion of an additional linguistic task might have made the cognitive load more comparable between the groups. Moreover, adding an additional linguistic task could have helped to better understand the specific role of the left vOT in the language processing of blind participants.

The fact that the current research design did not include semantic tasks makes it impossible to test for functions other than phonological processing in the vOT. Because of that, a complete interpretation of the observed pattern of activity in the left vOT is not possible based on the current findings.

When it comes to the task used in Study 2, the control condition included the presentation of real words. This may have evoked some, however only low-level, phonological processing. Additionally, the reaction times analysis has shown that the control task was easier for the participants than the experimental task. Thus, the effect of condition may not have been related solely to the different cognitive processes employed but also to the task difficulty. Adding an additional non-linguistic control condition would facilitate the interpretation of the results.

Finally, no separate localizer for the individual ROIs in temporal and frontal phonology-specific regions was used. The language localizer data could not be used for this purpose because, as already mentioned, the passive task did not evoke enough activity in the language regions, especially in the sighted group. Individual ROIs might have been more sensitive to group differences, but, because the used task consisted of only one run per condition, it was not possible to construct independent localizers for these regions.

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Appendix

Study 1: Analyses excluding early blind participants

Two subjects from the blind group lost their sight at age of two or three and were not congenitally blind. We conducted group-level analyses to see if the exclusion of these two participants changed something in the results. For reading sensitive (words > baseline) and reading specific (words > non-linguistic control) contrast we observed differences only in the cluster size (slightly smaller clusters for the congenitally blind subjects only), significantly activated regions remained the same. For pseudowords reading sensitive contrast (pseudowords > baseline), with the group restricted to the congenitally blind subjects activations were present in the same regions, though we observed slightly less activation in the occipital cortex (activation in right but not left calcarine and cuneus). For pseudowords reading specific contrast (pseudowords > non-linguistic control) in the restricted sample, the right inferior frontal cluster did not reach significance ($p_{cluster} = 0.052$ instead of $p_{cluster} = 0.007$ in the whole sample). For speech-sensitive contrast (words > baseline) activations were divided into more numerous clusters (five instead of three) and the activation in the right calcarine was not significant. In case of the speech specific contrast (words > non-linguistic control), the left vOT cluster did not reach significance ($p_{cluster} = 0.082$ instead of $p_{cluster} = 0.048$ in the whole sample). When it comes to speech-reading conjunction, in the restricted sample the right vOT cluster did not reach significance ($p_{cluster} = 0.096$ instead of $p_{cluster} = 0.013$ in the whole sample). We conclude that the differences between the results of the whole and restricted samples are mainly due to changes in the statistical power connected to a smaller sample.

Study 2: Analyses excluding early blind participants

Whole-brain results

Localizer

The activations for the reading-specific contrast (reading words > control) were present in bilateral vOT extending to the occipital cortex, bilateral IFG and pre/postcentral gyri as well as in SMA. Speech processing (speech words > control) invoked activation in the bilateral auditory (MTG, STG) cortex and vOT. The cluster in the left IFG observed on the total sample was present but did not survive cluster-level correction. The speech-reading conjunction was present in the bilateral vOT. Again, the left IFG cluster observed in the total sample was present but did not survive cluster-level correction.

When it comes to group differences, during reading congenitally blind subjects activated bilateral vOT extending to the occipital cortex and left IFG more than the sighted subjects. Clusters in the right IFG and SMA that were present in the comparison of the total blind sample and the sighted groups were present but did not survive cluster-level correction. The activations higher for the sighted group than for the congenitally blind group remained the same as for the complete sample. For speech processing, the group differences were practically the same as for the complete sample. The only difference was the significance of the right IPL cluster in the sighted > congenitally blind comparison, which did not survive the cluster-level correction.

Phonological task

The activations during phonological processing (rhyming > baseline) were almost identical for the congenitally blind group and the total sample. Congenitally blind subjects activated the occipital cortex to a larger extent than the sighted subjects. Sighted subjects presented higher activation in the bilateral middle cingulate than the congenitally blind group. Activations during the control task were also very similar in the congenitally and the total blind sample, as were the regions of the group differences with the sighted group. The regions of significant deactivation during both the rhyming and control task were also very similar to the complete sample.

The rhyming > control contrast again invoked very similar, however a little bit less extensive activations in the congenitally blind group and the total sample. The significant difference between the sighted and congenitally blind subjects for this contrast was again present in the left vOT on the lenient statistical threshold ($p < 0.001$, cluster extent = 50 voxels).

ROI analyses

Group and condition effects in the left vOT ROIs

For the literature-based ROI the robust two-way mixed ANOVA gave significant main effect of group ($F(1, 35.49) = 39.90$, $p < 0.001$), main effect of condition ($F(1, 38.58) = 44.62$, $p < 0.001$) and a significant group by condition interaction ($F(1, 38.58) = 5.75$, $p = 0.021$). The results were thus very similar to the results of the whole group, with the difference in the significance of the interaction. The correlations with the reading skills were a little bit weaker than in the whole sample and the correlation with the rhyming task activation was only marginally significant (*rho* = 0.34, $p = 0.064$).

When the individual ROIs were considered, the main effect of group ($F(1, 36.94) = 47.89$, $p < 0.001$) and condition ($F(1, 46.86) = 36.97$, $p < 0.001$) were observed. As was the case in the whole sample, the group x condition interaction was insignificant ($F(1, 46.86) = 2.36$, $p = 0.131$). There was a significant correlation between the rhyming task activation and reading skills (*rho* = 0.43, $p = 0.018$) but the correlation with the control task activation was insignificant (*rho* = 0.27, $p = 0.168$). The correlation between reading and non-linguistic auditory stimuli processing (vocoded speech), remained insignificant (*rho* = 0.00, $p = 0.983$).

Comparison to the other language-network ROIs

The results of the three-way mixed ANOVA conducted with only congenitally blind subjects were the same as for the analysis of the complete sample. There was main effect of group ($\chi^2(1) = 9.30$, $p = 0.002$), ROI ($\chi^2(3) = 526.58$, $p < 0.001$) and condition ($\chi^2(1) = 26.23$, $p < 0.001$), as well as significant group by ROI interaction ($\chi^2(3) = 45.66$, $p < 0.001$). The condition by group, condition by ROI and condition by ROI by group interactions were not significant.

Post-hoc tests have shown that the activations for rhyming were higher than for control task in both groups, for the STG and V1, and in case of the sighted subjects vOT ROIs (Blind: V1: $p = 0.012$, STG: $p = 0.019$; Sighted: V1: $p = 0.012$, STG: $p = 0.019$, vOT: $p = 0.040$), but this difference became insignificant for Broca’s area and in case of the blind subjects the vOT ROIs (Blind: vOT: $p = 0.128$, Broca’s area: $p = 0.077$, Sighted: Broca’s area: $p = 0.077$).

Group by ROI interaction can be interpreted as stemming from the fact that in the occipital ROIs (Rhyming: V1: $p = 0.050$, vOT: $p < 0.001$, Control: V1: $p = 0.050$, vOT: $p < 0.001$), for both conditions, activation was higher in the blind group than in the sighted group and the differences between the groups were not significant for the Broca’s area (Rhyming: $p = 0.844$, Control: $p = 0.844$) and STG ROI (Rhyming: $p = 1.000$, Control: $p = 1.000$). In the blind group, for both conditions, STG ROI activation was higher than the three other ROIs (p-values of all comparisons < 0.001) and the differences between the Broca’s area, V1 and vOT were insignificant. In the sighted group on the other hand, for both conditions, not only STG ROI had higher activation than the three other ROIs (p-values of all comparisons < 0.001) but also the Broca’s area had higher activation than the vOT ROI ($p < 0.001$). The differences between the vOT and V1, as well as V1 and Broca’s area, were not significant.

Study 3: Analyses on the original data without missing data imputation

Group differences

As some of the variable's distribution diverged from normal, Mann's-Whitney's *U* was used to compare the groups with Bonferroni-Holm correction for multiple comparisons. Sighted subjects achieved higher scores in words and pseudowords reading, perceptual speed, rapid naming (letters) and orthographic awareness. Blind participants scored higher in phonological awareness, rapid naming (textures), tactile acuity and working memory. The exact results of the analysis are presented in Table A1. There were no discrepancies between the group differences when the analyses were performed on the original and imputed datasets.

Table A1. Group comparison with the descriptive statistics within groups on the original dataset.

		Mean	SD	Median	Min	Max	Skewness	Kurtosis	*W*	*p*	*U*	*p*
READ_WORDS	Blind	24.32	11.06	25.33	5.55	56.86	0.55	3.26	0.96	0.128	141.000	< 0.001
	Sighted	53.99	13.24	52.93	15.50	76.79	-0.49	3.05	0.97	0.228		
READ_PSEUDOWORDS	Blind	27.96	12.93	27.87	3.28	56.42	0.37	2.82	0.97	0.199	188.000	< 0.001
	Sighted	62.12	19.08	60.36	21.12	99.78	-0.02	2.17	0.98	0.598		
PA	Blind	-43.43	30.20	-31.00	-151.00	-14.00	-1.91	6.75	0.78	0.000	168.000	< 0.001
	Sighted	-14.17	7.97	-12.00	-40.00	-6.00	-1.89	6.30	0.78	0.000		
Perceptual Time	Blind	0.15	0.09	0.12	0.02	0.41	0.79	2.96	0.94	0.010	226.000	< 0.001
	Sighted	0.51	0.24	0.52	0.10	0.97	0.00	1.90	0.96	0.097		
RAN (Textures)	Blind	-71.35	43.49	-58.00	-263.00	-36.00	-2.87	12.05	0.66	0.000	1582.500	< 0.001
	Sighted	-93.36	26.79	-86.50	-162.00	-55.00	-0.56	2.35	0.92	0.006		
RAN (Letters)	Blind	-31.17	14.41	-28.00	-84.00	-14.00	-1.75	6.04	0.82	0.000	716.500	< 0.001
	Sighted	-21.82	5.83	-21.00	-38.00	-12.00	-0.76	3.19	0.95	0.021		
GOT	Blind	-2.83	1.35	-2.31	-6.00	-1.25	-1.32	3.54	0.80	0.000	1389.500	< 0.001
	Sighted	-4.29	1.65	-4.50	-6.00	-1.43	0.28	1.45	0.84	0.000		
Digit Span	Blind	15.58	4.86	15.00	6.00	27.00	0.34	2.59	0.97	0.284	1830.000	0.004
	Sighted	12.71	3.48	13.00	6.00	20.00	0.08	2.65	0.97	0.211		
Orthographic Sensitivity	Blind	6.65	3.34	6.96	0.15	11.36	-0.25	2.00	0.95	0.057	1467.000	0.003
	Sighted	4.61	3.03	4.22	0.07	10.54	0.41	2.31	0.95	0.044		

Relationship with age

As the distribution of several variables diverged from normal, Spearman's correlation coefficient was used. Examination of the scatter plots depicting the relationship between age and literacy skills suggested a non-linear, logarithmic relationship. Thus, the correlation with the natural logarithm of age was tested, instead of the correlation with age. All of the correlations with age were significant apart from the correlations with tactile acuity, RAN Textures and PA (trend level) in the blind group. The detailed results of the correlation analysis are presented in Table A2. The correlations were compared between the sighted and the blind using the bootstrap comparison. P-values from these comparisons are also presented in Table A2. None of the correlations were significantly different between the blind and the sighted.

Table A2. Spearman's correlations with age and literacy-related variables. *P*-values after Bonferroni-Holm correction presented.

	Blind		Sighted		
	rho	*p*	*rho*	*p*	Bootstrap *p*
READ_WORDS	0.62	<0.001	0.52	<0.001	2.155
READ_PSEUDOWORDS	0.60	<0.001	0.51	<0.001	2.132
PA	0.34	0.075	0.59	<0.001	1.022
Perceptual speech	0.50	<0.001	0.64	<0.001	1.950
RAN Letters	0.48	<0.001	0.42	0.006	1.478
RAN Textures	0.29	0.110	0.58	<0.001	0.816
Digit Span	0.43	0.004	0.33	0.036	1.659
GOT	-0.09	0.561	0.35	0.020	0.423
Orthographic Sensitivity	0.62	<0.001	0.63	<0.001	0.897

Reading predictors across groups

The influence of group (Sighted vs Blind), phonological awareness, rapid naming (letters), working memory, tactile acuity on the reading level (of words or pseudowords) was tested using linear regression ("lm" function). Models explained 73% for words and 81% for pseudowords of the reading skill variability (measured with adjusted R^2). For both words and pseudowords reading, group and rapid letter naming turned out to be the significant predictors (Table A3, Table A4). In both models, there was a significant group by phonological awareness interaction that indicated that phonological awareness is a significant predictor of reading skill in the sighted but not in the blind group (Figure A1, Figure A2).

Table A3. The linear regression results with words reading (READ_WORDS) as the dependent variable, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**32.03**	**12.62**	**51.45**	**0.00**	**3.30**	**0.002**	**NA**
Group	**35.45**	**7.39**	**63.50**	**0.97**	**2.52**	**0.014**	**0.56**
PA	-0.25	-1.34	0.84	-0.05	-0.46	0.644	0.07
RAN Letters	**0.63**	**0.26**	**1.01**	**0.36**	**3.36**	**0.001**	**0.08**
Digit Span	0.51	-0.30	1.31	0.12	1.26	0.213	0.00
GOT	-2.09	-5.27	1.10	-0.19	-1.31	0.195	0.00
Group * PA	**2.55**	**0.68**	**4.42**	**0.45**	**2.73**	**0.008**	**0.03**
Group * RAN Letters	0.04	-0.63	0.72	0.03	0.13	0.898	0.00
Group * Digit Span	-1.04	-2.61	0.53	-0.39	-1.32	0.192	0.01
Group * GOT	2.99	-0.78	6.76	0.40	1.58	0.118	0.01

R^2 adjusted = 0.73

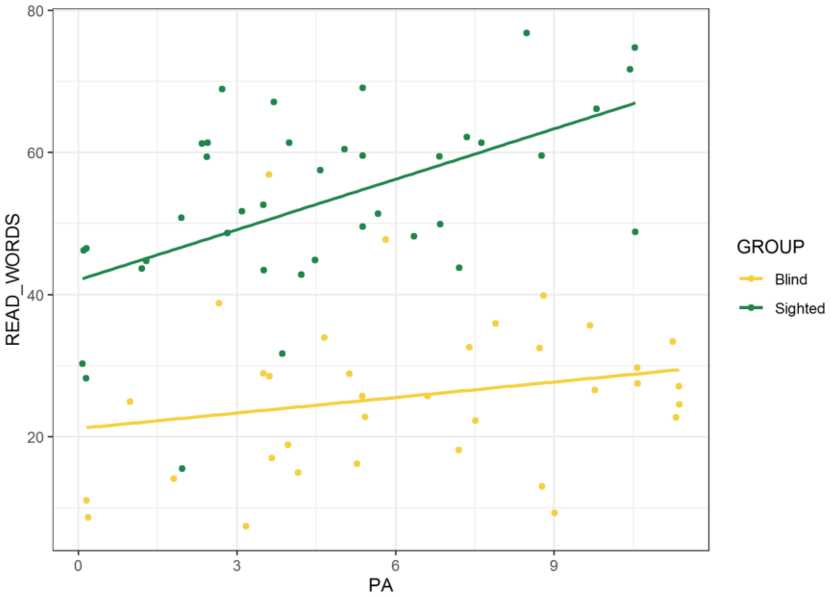

Figure A1. Group by PA interaction in the regression with READ_WORDS as the dependent variable on the original dataset. READ_WORDS scores are plotted as a function of PA scores with regression lines within groups.

Table A4. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**29.05**	**8.49**	**49.61**	**0.00**	**2.82**	**0.006**	**NA**
Group	**45.32**	**15.60**	**75.04**	**0.98**	**3.05**	**0.003**	**0.52**
PA	0.41	-0.74	1.56	0.06	0.71	0.479	0.17
RAN Letters	**0.51**	**0.11**	**0.90**	**0.23**	**2.54**	**0.014**	**0.06**
Digit Span	0.74	-0.11	1.60	0.14	1.74	0.086	0.01
GOT	-0.50	-3.87	2.88	-0.04	-0.29	0.770	0.00
Group * PA	**4.18**	**2.20**	**6.16**	**0.58**	**4.22**	**< 0.001**	**0.06**
Group * RAN Letters	0.65	-0.07	1.36	0.33	1.80	0.077	0.01
Group * Digit Span	-1.38	-3.05	0.28	-0.41	-1.66	0.101	0.01
Group * GOT	0.44	-3.56	4.43	0.05	0.22	0.828	0.00

R^2 adjusted = 0.81

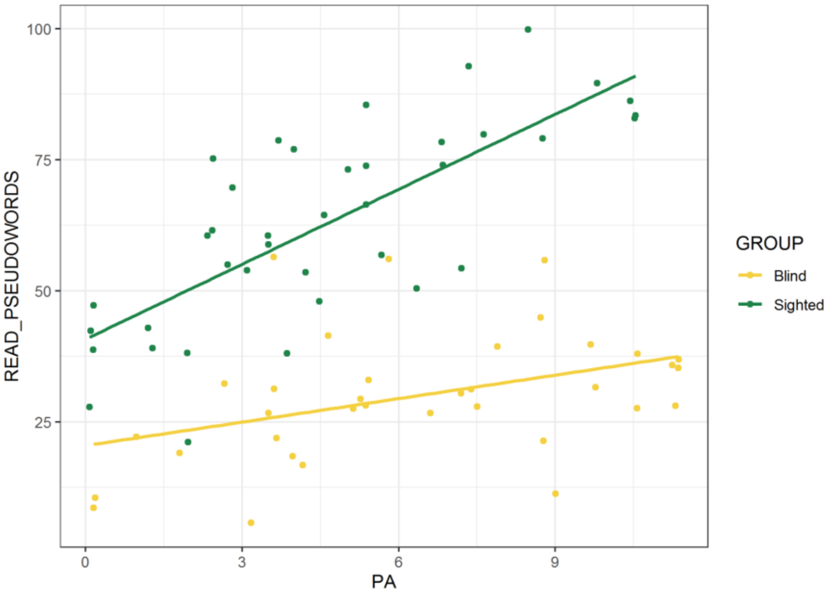

Figure A2 GROUP * PA interaction in the regression with READ_PSEUDOWORDS as the dependent variable on the original dataset. READ_PSEUDOWORDS scores are plotted as a function of PA scores with regression lines within groups.

Reading predictors within groups

The influence of PA, RAN Letters, Digit Span and GOT on the reading level was tested within the groups using linear regressions ("lm" function). When words reading was the dependent variable, only rapid letter naming turned out to be a significant predictor of the reading level in the blind group (Table A5). The model explained 43% of the word reading variance.

Table A5. The linear regression results with words reading (READ_WORDS) as the dependent variable in the blind group, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**32.03**	**14.77**	**49.29**	**0.00**	**3.79**	**0.001**	**NA**
PA	-0.25	-1.22	0.72	-0.08	-0.53	0.598	0.05
RAN Letters	**0.63**	**0.30**	**0.97**	**0.73**	**3.87**	**0.001**	**0.38**
Digit Span	0.51	-0.21	1.22	0.23	1.45	0.159	0.03
GOT	-2.09	-4.92	0.74	-0.25	-1.51	0.142	0.04

R^2 adjusted = 0.43

Contrary, in the sighted group RAN Letters and PA were both significant predictors of the word reading skill (Table A6). The model explained 36% of the word reading variability.

Table A6. The linear regression results with words reading (READ_WORDS) as the dependent variable in the sighted group, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**67.48**	**44.77**	**90.19**	**0.00**	**6.04**	**< 0.001**	**NA**
PA	**2.30**	**0.60**	**4.01**	**0.53**	**2.74**	**0.010**	**0.30**
RAN Letters	**0.68**	**0.04**	**1.31**	**0.32**	**2.17**	**0.037**	**0.11**
Digit Span	-0.53	-2.04	0.98	-0.14	-0.71	0.481	0.01
GOT	0.90	-1.36	3.16	0.11	0.81	0.425	0.01

R^2 adjusted = 0.36

When pseudowords reading was treated as the dependent variable, only RAN Letters was a significant predictor of the reading outcomes in the blind group (Table A7). Digit span was significant only on the trend level (p = 0.056). Forty-nine percent of pseudowords reading variance was explained.

Table A7. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable in the blind group, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**29.05**	**10.61**	**47.49**	**0.00**	**3.22**	**0.003**	**NA**
PA	0.41	-0.62	1.45	0.11	0.81	0.423	0.17
RAN Letters	**0.51**	**0.15**	**0.86**	**0.52**	**2.89**	**0.007**	**0.32**
Digit Span	0.74	-0.02	1.51	0.30	1.99	0.056	0.06
GOT	-0.50	-3.52	2.53	-0.05	-0.34	0.740	0.00

R^2 adjusted = 0.49

In the sighted group, similarly as it was the case in the model with words reading as the dependent variable, PA, as well as RAN Letters turned out to be the significant predictors of reading level (Table A8). The model explained 66% of the pseudowords reading variance.

Table A8. The linear regression results with pseudowords reading (READ_PSEUDOWORDS) as the dependent variable in the sighted group, original dataset.

	Beta	CI low	CI high	β	*t*	*p*	R^2 change
(Intercept)	**74.37**	**50.43**	**98.31**	**0.00**	**6.31**	**< 0.001**	**NA**
PA	**4.59**	**2.79**	**6.39**	**0.73**	**5.19**	**< 0.001**	**0.57**
RAN Letters	**1.15**	**0.49**	**1.82**	**0.38**	**3.51**	**0.001**	**0.12**
Digit Span	-0.64	-2.23	0.95	-0.12	-0.82	0.420	0.01
GOT	-0.06	-2.44	2.33	-0.01	-0.05	0.960	0.00

R^2 adjusted = 0.66

Study 3: Analysis of the variability in the PA tests

The analyses were conducted on the original dataset (missing data omitted). For Spoonerisms, the score was divided by the maximal number of items in the test (thus, the maximal score). The results of the variability analysis are presented in Table A9. As it can be seen, the coefficient of variation of the results for all the tests was similar between the two groups. Additionally, for the Vowel Replacement and Phoneme Deletion test blind group's results approached the ceiling effect (group mean above 90%, low coefficients of variation).

Table A9. Variability of the results in the phonological tasks

		Mean	SD	Coefficient of variation
Vowel Replacement Accuracy (%)	Blind	97.17	9.31	0.10
	Sighted	94.95	8.75	0.09
Vowel Replacement Time	Blind	38.57	18.34	0.48
	Sighted	52.42	22.36	0.43
Phoneme Deletion Accuracy (%)	Blind	91.14	14.82	0.16
	Sighted	85.82	15.72	0.18
Phoneme Deletion Time	Blind	116.54	35.04	0.30
	Sighted	151.75	51.43	0.34
Spoonerisms (%)	Blind	57.23	31.17	0.30
	Sighted	41.13	27.92	0.34