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**Metamodal Reading in Sighted and Blind Adults:
Longitudinal and Cross-Sectional fMRI of Braille Reading**

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Abstract

Whether the adult reading network is metamodally organised remains debated, particularly regarding the role of left ventral occipitotemporal cortex, including the visual word form area (VWFA), in processing written stimuli presented visually or tactually. This dissertation tested whether Braille reading recruits a shared reading network that is also engaged during visual print reading, while still showing differences shaped by input route, task demands, training stage, and sensory experience. Sighted adults were assigned either to a Braille-learning group ($N = 17$) or to a passive control group ($N = 19$). Additionally, a separate group of blind Braille readers participated in a single cross-sectional session ($N = 21$). The experimental battery comprised three block-design lexical decision tasks - visual reading of Polish print, visual reading of Braille strings, and tactile reading of Braille strings - as well as a non-linguistic tactile six-dot detection task. Measurements were repeated during the early and later stages of training. Longitudinally, within the learning group, task-related activation increased relative to the pre-training baseline in both Braille lexical decision tasks. Recruitment of the inferior frontal gyrus was observed after 7 days of Braille training in both tasks, whereas recruitment in the left ventral occipitotemporal cortex, including the VWFA region, was detected after 7 days during visual Braille reading and emerged during tactile Braille reading by approximately 6 weeks. Later post-baseline pairwise comparisons did not show further significant increases. Within-subject conjunction analyses across all three reading tasks identified a left-lateralised core of the reading network, including the inferior frontal gyrus and left ventral occipitotemporal cortex, while both Braille tasks additionally engaged parietal, dorsal occipital, cerebellar, and subcortical regions. In the perceptual tactile six-dot detection task, Braille learners, despite behavioural performance comparable to that of passive controls, showed stronger activation in primary sensorimotor cortices, parietal regions, the inferior frontal gyrus, thalamus, striatum, and cerebellum, indicating greater engagement of reading-relevant and sensorimotor-attentional networks during a task that did not explicitly require reading. Because the corresponding statistical model yielded no main effect of time and no time-by-group interaction, these data do not establish when the learner-control differences emerged; they show only that Braille learners exhibited stronger task-related activation than passive controls when averaged across sessions. In the cross-sectional analysis, blind Braille readers showed stronger occipital recruitment, whereas sighted learners showed greater engagement of frontoparietal control and sensorimotor networks. Together, these findings support shared recruitment of a left-lateralised core of the

reading network across visual print and Braille, while indicating that its broader implementation depends on input route, task demands, training stage, and sensory experience.

Streszczenie

Przedmiotem sporu pozostaje to, czy sieć czytania u dorosłych ma charakter metamodalny, zwłaszcza w odniesieniu do roli lewej brzusznej kory potyliczno-skroniowej, obejmującej obszar określany w literaturze jako obszar wzrokowej formy słów (ang. visual word form area, VWFA), w przetwarzaniu bodźców pisanych prezentowanych wzrokowo lub dotykowo. Celem rozprawy było sprawdzenie, czy czytanie tekstów zapisanych alfabetem Braille’a angażuje wspólną sieć czytania aktywną zarówno podczas czytania wzrokowego, jak i dotykowego, przy jednoczesnym zachowaniu różnic zależnych od drogi wejścia bodźca, rodzaju zadania, etapu treningu i doświadczenia wzrokowego. Widzących dorosłych przydzielono do grupy uczącej się alfabetu Braille’a ($N = 17$) albo do pasywnej grupy kontrolnej ($N = 19$), a odrębną grupę stanowili niewidomi czytelnicy alfabetu Braille’a badani jednorazowo ($N = 21$). Zastosowano trzy blokowe zadania decyzji leksykalnej: wzrokowe czytanie polskiego druku w alfabecie łacińskim, wzrokowe czytanie ciągów znaków zapisanych alfabetem Braille’a oraz dotykowe czytanie ciągów znaków zapisanych alfabetem Braille’a. Dodatkowo zastosowano niejęzykowe dotykowe zadanie wykrywania układu sześciu punktów. Pomiary powtarzano na wczesnych i późniejszych etapach treningu, aby scharakteryzować dynamikę zmian.

W badaniu podłużnym w grupie uczącej się alfabetu Braille’a stwierdzono, że w obu zadaniach decyzji leksykalnej dotyczących bodźców zapisanych alfabetem Braille’a aktywacja związana z zadaniem wzrastała względem poziomu bazowego sprzed treningu. Zaangażowanie zakrętu czołowego dolnego było obecne już po 7 dniach treningu w obu zadaniach wykorzystujących alfabet Braille’a, natomiast zaangażowanie lewej brzusznej kory potyliczno-skroniowej, w tym obszaru VWFA, było widoczne po 7 dniach podczas czytania wzrokowego znaków Braille’a, a podczas czytania dotykiem pojawiało się po około 6 tygodniach treningu. Późniejsze porównania między punktami pomiarowymi po pomiarze bazowym nie wykazały dalszych istotnych zmian. Analizy koniunkcji wewnątrzosobniczej dla wszystkich trzech zadań czytania ujawniły lewostronnie zlokalizowany rdzeń sieci czytania, obejmujący zakręt czołowy dolny oraz lewą brzuszną korę potyliczno-skroniową, natomiast oba zadania wykorzystujące alfabet Braille’a dodatkowo angażowały obszary ciemieniowe, grzbietowo-potyliczne, mózdzkowe i podkorowe. W dotykowym zadaniu percepcyjnym polegającym na wykrywaniu układu sześciu punktów osoby uczące się, mimo porównywalnych wyników behawioralnych, wykazywały silniejszą niż pasywna grupa kontrolna aktywację w pierwszorzędowych obszarach czuciowo-ruchowych, obszarach

ciemieniowych, zakręcie czołowym dolnym, wzgórzu, prążkowi i mózdzku, co wskazuje na większe zaangażowanie procesów związanych z czytaniem oraz procesów czuciowo-ruchowych i uwagowych podczas zadania, które nie zawierało jawnego wymogu czytania. Ponieważ odpowiadający temu zadaniu model statystyczny nie wykazał ani głównego efektu czasu, ani interakcji $\text{czas} \times \text{grupa}$, dane te nie pozwalają określić, kiedy pojawiły się różnice między osobami uczącymi się alfabetu Braille'a a pasywną grupą kontrolną; wskazują natomiast, że po uśrednieniu między sesjami osoby uczące się wykazywały silniejszą aktywację związaną z zadaniem niż grupa kontrolna.

W badaniu przekrojowym niewidomi czytelnicy alfabetu Braille'a wykazywali silniejsze zaangażowanie kory potylicznej, natomiast widzący uczący się alfabetu Braille'a wykazywali większe zaangażowanie sieci czołowo-ciemieniowej oraz czuciowo-ruchowej. Uzyskane wyniki wspierają tezę o wspólnym zaangażowaniu lewostronnego rdzenia sieci czytania podczas czytania druku i tekstów zapisanych alfabetem Braille'a, a zarazem wskazują, że szerszy wzorzec aktywacji tej sieci zależy od drogi wejścia bodźca, wymagań zadania, etapu treningu oraz doświadczenia wzrokowego.

Abbreviations

Table 1. The list of abbreviations used in the thesis and their meanings.

<i>Abbreviation</i>	<i>Meaning</i>
AAL	Automated Anatomical Labeling
ANOVA	Analysis of variance
BIDS	Brain Imaging Data Structure
BOLD	Blood-oxygenation-level-dependent
CSF	Cerebrospinal fluid
DD6	Braille 6-dot Detection Task
FA	Fractional anisotropy
FD	Framewise displacement
fMRI	Functional Magnetic Resonance Imaging
FWE	Family-wise error
FWHM	Full Width at Half Maximum
GLM	General linear model
GM	Grey matter
IFG	Inferior frontal gyrus
ISI	Inter-stimulus interval
L1	Native (Polish) language
LDT	Lexical Decision Task
MNI	Montreal Neurological Institute (brain template)
MRI	Magnetic resonance imaging
rmANOVA	Repeated measures analysis of variance
ROI	Region of interest
rTMS	Repetitive Transcranial Magnetic Stimulation
S1	Primary somatosensory cortex
SRef	Single-band reference
SD	Standard deviation
SPM	Statistical Parametric Mapping
T _{1w}	T ₁ -weighted image
TE	Echo time
TI	Inversion time
TMS	Transcranial Magnetic Stimulation
TP	Time point
TR	Repetition time
vOTC	Ventral occipitotemporal cortex
VWFA	Visual Word Form Area
WM	White matter

1. Introduction

1.1. Introduction to neuroplasticity

The human brain is capable of change across the lifespan (Diniz & Crestani, 2023). Every experience and stimulus we encounter can induce a neuroplastic response at the functional or structural brain level (Magee & Grienberger, 2020). However, it was only in the 19th century that the brain became central to what we now call modern neuroscience (Cecala, 2013). William James was the first to use the term plasticity in a way that aligns with today's modern perception of the concept (James et al., 1890; Puderbaugh & Emmady, 2025). He theorised that brain plasticity is linked to activity, and that specific behaviours engage distinct neural pathways. Santiago Ramón y Cajal later proposed that brain plasticity could be observed when intensive mental processes, which increase brain activity, give rise to structural changes in the brain, specifically new connections between cortical neurons (Ramón y Cajal, 1894). He defined the neuron as a primary anatomical, physiological, genetic, and metabolic unit, the key to understanding the nervous system's organisation (Ramón y Cajal, 1894; Shepherd, 2015). Jerzy Konorski further proposed in 1948 that learning induces changes on the morphological level in neural synaptic connections (Konorski, 1948). He stated that creating entirely new connections was not crucial. Instead, he highlighted that the existing but unused pathways change as a result of the coactivation of neural centres. Similar concepts were presented by Hebb, who proposed that cells in the vicinity form assemblies and that once a cell fires and engages another, the two become associated. Due to growth or a metabolic process, they increase their efficiency (Hebb, 1949).

Nowadays, neuroplasticity is defined as the brain's ability to reorganise and adapt to constantly changing environmental inputs or the brain's capacity for change in terms of its efficiency or functions (Diniz & Crestani, 2023; Marzola et al., 2023). This dynamic process underlies various cognitive functions such as learning or memory (Magee & Grienberger, 2020). In recent years, significant advancements in neuroimaging techniques and computational modelling have facilitated the development of network-based models of brain organisation, emphasising the importance of large-scale functional connectivity in determining neuroplastic changes (Bassett & Sporns, 2017; Parkes et al., 2024). These models underscore the crucial role of experience-dependent processes in shaping the brain's organisation, providing a framework for understanding the neural basis of individual differences, cognitive abilities, and potential therapeutic interventions (H.-J. Park & Friston, 2013; Valk et al., 2023). Finally, plasticity spans timescales and mechanisms, including

synaptic modification, dendritic spine remodelling, and, across species, adult neurogenesis (with ongoing debate about its extent in humans) (Alonso et al., 2024; Kasai, 2023; Magee & Grienberger, 2020).

1.2. The neuroplastic process of reading

Reading is a paradigmatic case of experience-dependent plasticity. Unlike spoken language, which typically emerges without explicit instruction, literacy is a culturally recent invention that must be taught and practised (Dehaene & Cohen, 2011). Within a few years of instruction, the human brain acquires a new ability, rapid identification of orthographic patterns and their mapping to phonological and semantic codes, by repurposing and fine-tuning existing visual and language circuitry (Dehaene et al., 2015). Converging behavioural and neuroimaging evidence indicates that as children or illiterate adults learn to read, a region of left ventral occipitotemporal cortex (vOTC) becomes selectively responsive to letter strings and words; this area is widely referred to as the visual word form area (VWFA) (Cohen et al., 2002; McCandliss et al., 2003). The neuronal recycling account proposes that literacy adapts pre-existing cortical resources, optimised initially for complex object and shape processing, to the demands of orthography, constrained by the region's connectivity to language systems (Dehaene & Cohen, 2011).

Functional MRI (fMRI) studies have documented this transformation. In literate adults, words and pronounceable pseudowords reliably activate the VWFA and a left-lateralised fronto-temporo-parietal language network; in contrast, illiterate adults or beginning readers show weaker vOTC engagement and a heavier reliance on effortful phonological and control systems (Dehaene et al., 2010; Martin et al., 2015). Learning to read also sharpens visual perceptual tuning in ways that facilitate orthographic processing (e.g., reductions in mirror generalisation for letters), consistent with functionally specific plasticity at intermediate stages of the ventral visual stream (Pegado et al., 2014). Crucially, literacy-related plasticity is not confined to childhood: although early development is a sensitive period for aspects of language and vision, adult learners can acquire basic literacy and develop task-evoked activation patterns that increasingly resemble those of proficient readers, albeit sometimes with slower time courses and greater inter-individual variability (Abutalebi et al., 2007).

In summary, reading provides a tractable model of human experience-driven cortical reorganisation: a culturally learned skill that builds a specialised visual–language interface in the left vOTC and reshapes the engagement of distributed language networks.

1.3. Magnetic Resonance Imaging as a key method for understanding neuroplasticity in the human brain.

The methodological developments in neuroscience over the last 40 years have enabled a non-invasive in vivo investigation of the human brain to measure the spatial and temporal patterns of experience-dependent neuroplasticity using various paradigms (Uğurbil, 2021; Yen et al., 2023). Modern neuroimaging techniques provide a wide range of information about the characteristics of brain activity (Logothetis, 2008; Uludağ, 2023). Functional Magnetic Resonance Imaging (fMRI) is one of the most frequently used methods for examining the brain's functional response (Glover, 2011). This method uses T2*w images to measure metabolic activity and variability in the brain's oxygen demand (Wager et al., 2015). It uses the blood-oxygen-level-dependent (BOLD) method to measure functional brain activity (Hillman, 2014; Ogawa et al., 1990). Neural signalling in the brain and the processes underlying it, such as the generation and propagation of action potentials, vesicle binding at the presynaptic junction, or the regeneration of action potentials in postsynaptic structures, use energy from adenosine triphosphate (Glover, 2011; Watts et al., 2018). It is produced from the glycolytic oxygenation of glucose, mainly done by the mitochondria. Its byproduct is carbon dioxide (Magistretti & Allaman, 2018; Watts et al., 2018). During a cognitive task, such as tactile reading, increased neuronal and synaptic activity raises local energy demand and the cerebral metabolic rate of oxygen consumption (CMRO₂) (Buxton and Frank 1997; Schaeffer and Iadecola 2021). In response, signalling within the neurovascular unit induces vasodilation in upstream arterioles and increases local cerebral blood flow (Hillman 2014). In the canonical positive BOLD response, the increase in blood flow typically exceeds the increase in oxygen consumption (Buxton and Frank 1997; Davis et al. 1998). As a result, the local concentration of deoxygenated haemoglobin decreases relative to oxygenated haemoglobin; because deoxygenated haemoglobin is paramagnetic, whereas oxygenated haemoglobin is diamagnetic, this shift increases the T2*-weighted MR signal measured with fMRI (Biondetti et al. 2023; Uludağ 2023). These coupled changes in blood oxygenation and blood volume unfold over seconds and constitute the haemodynamic response that underlies the BOLD signal (Buxton et al. 1998). The whole process is the haemodynamic response to an event on a neural level. While the neural response lasts milliseconds, the hemodynamic response gradually rises within 1-2 seconds, peaks in 4-6 seconds, and returns to baseline 12-20 seconds after stimulus onset (Poldrack et al., 2011).

1.4. The reading system and the visual word form area

Neuroimaging, lesion, and electrophysiological evidence converge on a distributed reading network consisting of a ventral occipitotemporal pathway for orthographic processing, a temporo-parietal system supporting grapheme-to-phoneme mapping and phonological short-term memory, and inferior frontal regions implicated in phonological/lexical selection, articulatory planning, and controlled retrieval (Jobard et al., 2003; Price, 2012; Pugh et al., 2000). In fluent readers, this network is strongly left-lateralised and operates with remarkable efficiency, supporting rapid, largely automatic word identification (Martin et al., 2015).

The VWFA shows a preference for letter strings and words over low-level visual controls and non-orthographic objects in literate individuals (Dehaene et al., 2002; McCandliss et al., 2003). It abstracts over font, case, size, and position, coding identity at the level of sublexical letter combinations and word forms (Dehaene & Cohen, 2011). Classic neuropsychology underscores its necessity: lesions encompassing the left mid-fusiform gyrus can cause pure alexia (letter-by-letter reading) with relatively spared object recognition, consistent with a bottleneck for rapid word identification (Cohen et al., 2002).

The location and specialisation of the VWFA are likely constrained by connectivity. The region lies at the intersection of high-acuity foveal visual representations and long-range pathways to the language cortex. Diffusion-MRI tractography reveals connections from the left vOTC to the left perisylvian areas, including the IFG and the superior temporal cortex (Bouhali et al., 2014). In pre-readers, the strength of these pre-existing connections predicts where VWFA selectivity will later emerge, implying that connectivity precedes function (Saygin et al., 2016). Computationally, the region's priors: sensitivity to line junctions and high-resolution shapes, plus access to phonological/semantic hubs, make it an apt cortical substrate to be recycled for orthography (Hannagan et al., 2015).

High-resolution fMRI indicates a posterior–anterior gradient within vOTC: a more posterior region linked to visual feature analysis and a more anterior region with stronger coupling to language regions and greater sensitivity to lexical factors (White et al., 2019; Yablonski et al., 2024). One of the previous proposals suggests a bidirectional exchange between visual input and top-down predictions from language systems, explaining context effects and rapid disambiguation during reading (Price & Devlin, 2011). Recent evidence indicates task-dependent increases in coupling between the VWFA and IFG during active word recognition, relative to passive viewing (White et al., 2023), consistent with top-down constraints during skilled reading.

1.5. Metamodal organisation and Braille reading

The metamodal hypothesis states that cortical territories are organised primarily by the computations they perform rather than strictly by the sensory modality of their inputs (Pascual-Leone & Hamilton, 2001). In the absence of a given modality, or when a new mapping is learned, areas can be driven by alternative inputs, provided the information is formatted for their preferred algorithm (Bedny, 2017).

In congenitally blind readers, Braille by touch activates the occipital cortex, including striate and extrastriate areas typically devoted to vision in sighted individuals (Büchel, Price, & Friston, 1998; Sadato et al., 1996). This cross-modal activation is functionally relevant: applying TMS to the occipital cortex disrupts Braille reading performance in blind individuals (Cohen et al., 1997). Critically, a word-selective region emerges in left vOTC at a locus analogous to the sighted VWFA, showing greater responses to Braille words than to matched tactile controls (Reich et al., 2011). Using sensory substitution that converts letters into sounds, the same VWFA responds to auditory letter shapes, suggesting abstract orthographic identities independent of input modality (Striem-Amit et al., 2012). At the same time, in congenitally blind adults, this fusiform territory also participates in higher-level language processing (e.g., complex spoken sentence processing), a role that is broader than in sighted individuals (Kim et al., 2017).

The extent of occipital recruitment depends on sensory experience: early visual deprivation permits the extensive reallocation of occipital cortex, including V1, to non-visual functions, whereas late-blind individuals typically show less occipital engagement for non-visual tasks than their congenitally blind peers (Bedny, 2017; Collignon et al., 2009). Recent large-scale work further indicates that blindness and reading modality (tactile vs auditory) together shape the topography of the reading network (Tian et al., 2023).

At the same time, sighted adults can learn Braille, and training results in functional changes. Short programmes emphasising tactile character discrimination increase activity in somatosensory and fronto-parietal regions (Debowska et al., 2016). With intensive training in tactile lexical decision, VWFA and language regions are recruited for tactile words, and TMS to VWFA impairs tactile lexical decisions, establishing a causal role for VWFA in Braille reading in the sighted (Siuda-Krzywicka et al., 2016). In sighted learners, the primary visual cortex (V1) generally remains visually dominated. V1 recruitment is characteristic of congenitally blind Braille readers and is limited or absent in trained sighted adults (Sadato et al., 1996). Short-term sensory deprivation provides further context: five days of blindfolding,

paired with tactile training, transiently increases occipital responsiveness to touch in sighted adults, an effect that reverses upon the return of vision (Merabet et al., 2008). Together, these findings support a connectivity-constrained metamodal account in which higher-order visual areas in left vOTC, by virtue of privileged access to language networks, can be co-opted for tactile orthography in adults. In contrast, the early visual cortex remains more modality-anchored unless vision is absent from early life (Hannagan et al., 2015).

In this dissertation, *modality* refers to the sensory channel through which orthographic input reaches the reader (print, visual Braille, or tactile Braille). The term *metamodal* is used in a restricted sense to denote shared recruitment of reading-related regions across modalities; it does not imply identical computations, complete modality independence, or insensitivity to sensory experience. Sensory experience refers to the participant's long-term developmental and experiential background regarding visual input and tactile reading, including congenital blindness versus typical visual development, and extensive versus recent Braille experience.

1.6. Models of neuroplasticity dynamics

Building on the historical and conceptual overview above, contemporary work asks not only what changes with experience but also how plastic changes unfold over time in adult learners. For reading-like skills that combine perceptual analysis with language and decision processes, five complementary mechanisms have gained prominence: rapid prediction and error-minimisation that support emergent automaticity; synaptic regulation that stabilises new mappings; brief shifts in inhibitory tone that open windows for reorganisation; slower structural adaptations that improve transmission efficiency; and large-scale network reconfiguration constrained by the brain's wiring (Bassett & Sporns, 2017; H.-J. Park & Friston, 2013). Complementing these mechanisms, Lövdén's framework emphasises that adult plasticity is triggered when environmental demands exceed current functional supplies, leading to changes in processing efficiency and/or representations; this demand-supply principle implies dose-sensitive, challenge-dependent plasticity in our paradigms (Lövdén et al., 2010, 2013). As proficiency increases, higher-order language regions exert top-down constraints that shape ventral occipitotemporal representations, accelerating lexical access (Kuperberg & Jaeger, 2016; Y. Liu et al., 2021), and the cerebellum contributes learned timing predictions that further reduce processing latencies (D'Mello et al., 2020). In reading-like tactile tasks, this account predicts that tactile words increasingly recruit the left-lateralised orthography/language network typically engaged by print and that such recruitment becomes detectable even when attention is diverted; nonetheless, some accounts

emphasise that vOTC selectivity may arise through feature discovery without strong top-down prediction, motivating feedback-sensitive contrasts in our analyses (White et al., 2023). Repeated co-activation rapidly potentiates task-relevant assemblies, whereas slower homeostatic processes rescale excitability to preserve stable function and sharpen selectivity (Keck et al., 2017; Turrigiano, 2012); recent syntheses further highlight how this Hebbian-homeostatic interplay supports stable performance despite changing inputs (W. Wen & Turrigiano, 2024). In our longitudinal design, this translates to steep early improvements in speed/accuracy with increases in task-relevant responses or coupling, followed by stabilisation as practice continues; after a practice gap, partial attenuation (“forgetting”) is expected behaviourally and functionally, with rapid reacquisition upon re-exposure. Short-lived reductions in inhibitory tone can also transiently broaden the set of regions that participate in a task (e.g., parietal control areas, supplementary motor regions, and even occipital cortex during early tactile learning), after which inhibition is re-established as tuning consolidates (Kolasinski et al., 2019; H. Li et al., 2024); at the circuit level, disinhibitory mechanisms underpinning such effects have been reviewed in detail (Chéreau et al., 2022). Beyond fast functional change, repeated activity can modify oligodendroglial function and internode properties, tuning conduction velocity to improve spike-timing across engaged pathways; notably, these myelin-related adaptations typically lag functional plasticity and therefore serve here as supportive context rather than direct endpoints (Fields, 2015; Sampaio-Baptista & Johansen-Berg, 2017). At the systems level, practice is expected to shift functional topology from distributed, integrative patterns toward more focal, efficient modules centred on language/orthography regions, with corresponding changes in hub roles and inter-module coupling (Finc et al., 2020). In reading-like contexts, vOTC supports orthography-linked computations (Lerma-Usabiaga et al., 2018), and tactile engagement of the occipital/ventral pathways is plausible in both blind and temporarily sight-deprived adults (Merabet et al., 2008; Reich et al., 2011). Taken together, these principles yield concrete, fMRI + behavioural expectations for our study: early gains with selective stabilisation; a short-window broadening of recruitment followed by re-balancing; demand-sensitive session-to-session changes consistent with the supply-demand view; and network-level reconfiguration constrained by anatomy, with structural mechanisms acknowledged as longer-term background rather than direct outcomes in the present dataset.

1.7. Braille reading as a way of tracking the dynamics of training-induced cross-modal plasticity

Learning to read the Braille alphabet is a unique form of training, particularly valuable for studying neuroplasticity due to its strong connection to cross-modal plasticity (Lee, 2022; Saccone et al., 2024). Cross-modal plasticity, which occurs in response to the loss of a sensory function, involves two fundamental processes: the recruitment of the deprived sensory area to process the remaining senses, and compensatory plasticity, in which remaining sensory areas enhance their processing capabilities (Ewall et al., 2021). Widespread functional plasticity in adult sensory cortices following the loss of a sensory modality has been observed, forming the neural basis for cross-modal plasticity (Bavelier & Neville, 2002; Lee & Whitt, 2015; Merabet & Pascual-Leone, 2010). Enhanced abilities to discriminate auditory (Gougoux et al., 2004; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004), tactile (Grant et al., 2000; Van Boven et al., 2000) or olfactory (Cuevas et al., 2009; Renier et al., 2013) information have been documented in blind individuals. Research suggests that visual and tactile systems may employ similar cognitive processes, allowing humans to rely on a single modality to recognise objects when the other is absent (Tabrik et al., 2021). Moreover, compensatory cross-modal plasticity persists even after sight restoration, indicating that these brain changes last (Ewall et al., 2021).

Louis Braille introduced his alphabet in the nineteenth century to enable blind individuals to read through touch (Braille, 1829). Although Braille has undergone some modifications over time, it has remained essentially unchanged. The Braille system consists of a rectangle of six dots imprinted on paper, with different configurations representing specific letters or signs that can be read using the index finger.

Braille reading offers a unique opportunity to study cross-modal plasticity because it combines motor and sensory skills with linguistic components. This process engages basic motor and sensory regions, the language network, and brain regions associated with higher cognitive functions (Matuszewski et al., 2021). Evidence indicates that cross-modal plasticity occurs during Braille reading in blind individuals, as the visual cortex becomes active in response to tactile stimulation (Burton et al., 2004; Haupt et al., 2024).

Areas of the brain's reading network, particularly those related to visual processing, are active during Braille reading. Within the left ventral occipitotemporal cortex (vOTC), the visual word form area (VWFA) is a word-selective region implicated in rapid word and letter identification in sighted readers (Lerma-Usabiaga et al., 2018). This region becomes active in

both sighted adults reading visually and blind individuals reading through touch. (Reich et al., 2011). Notably, the activation pattern in these visual regions varies depending on the age at which an individual loses sight, indicating that neuroplastic processes are not limited by time (Büchel, Price, Frackowiak, et al., 1998). Cross-modal plasticity is not exclusive to individuals with irreversible sensory impairments. In healthy adults, temporary sensory deprivation, such as blindfolding, increases occipital activation during tactile discrimination tasks (Merabet et al., 2008).

One of the pioneering studies investigated the effects of a 3-week Braille reading course on brain structure and function (Debowska et al., 2016). Participants engaged in lessons to learn Braille characters and underwent MRI scans before and after the course. They performed a letter discrimination task and two non-linguistic control tasks during scanning. Increased activity was observed in brain regions associated with somatosensory processing and higher cognitive functions, along with increased fractional anisotropy in the somatosensory pathway and frontal and parietal-occipital areas. Notably, no decrease in fractional anisotropy was detected, indicating that structural and functional reorganisation can occur within a short period of just 3 weeks. However, the study has a limitation: the fMRI task may not be strictly linguistic or lexical in nature. The tasks focused on detecting and discriminating single letters and symbols, which could theoretically be performed with high accuracy even without prior knowledge of Braille.

To address the limitations identified in the previous study, a subsequent Braille study introduced a more demanding task, the Lexical Decision Task (LDT), designed to differentiate between reading- and somatosensory-specific activations (Siuda-Krzywicka et al., 2016). The experimental condition involved presenting sequences of 3-6 Braille letters, which could be either real words (e.g., “home”) or pseudowords that resemble real words but lack meaning (e.g., “bome”). In the control condition, participants were presented with sequences of Braille letters with no linguistic meaning, requiring only symbol detection. This design allowed for the isolation of reading-specific brain activations from those related solely to somatosensory processing. A comparable visual Braille LDT was also conducted as a control for the tactile task.

In addition to the LDT, participants underwent a nine-month tactile reading course, primarily focused on blindfolded self-practice. Participants trained daily using an A4 Braille sheet for 20 minutes, with progress monitored by qualified Braille teachers during monthly meetings. The course began with simple tactile recognition exercises and gradually introduced Braille

letters, eventually focusing on word reading. While the training emphasised tactile reading, participants also visually checked their responses, likely improving their visual Braille reading skills (Bola et al., 2016).

MRI scans were conducted before and after the course, similar to the previous study. The analysis revealed that the tactile reading task increased activity in several brain regions. Bilaterally, increased activation was observed in the inferior frontal gyrus, superior temporal gyrus, and precentral cortex. In the left hemisphere, additional activity was found in the fusiform gyrus, middle frontal gyrus, and middle temporal gyrus. In the right hemisphere, heightened responses were observed in the insula, cerebellum, and middle occipital gyrus. During the visual Braille task, increased activation was noted bilaterally in the prefrontal cortex and middle temporal gyrus, with further activity observed in the left hemisphere in the superior parietal lobule and middle frontal gyrus and in the right hemisphere in the superior temporal and frontal gyri. These regions are associated with processing sensory information related to touch and with higher-level cognitive functions involved in letter recognition and semantic processing.

A significant increase in activity was observed in the fusiform gyrus, which includes the visual word form area (VWFA) - a region typically associated with visual processing but here engaged in processing a non-visual stimulus. VWFA activity was also noted in the visual Braille task, though its level remained unchanged throughout the study, unlike the increase seen during tactile reading. These findings indicate that learning a complex skill, such as tactile Braille, over an extended period may lead to cross-modal plasticity in the brains of sighted individuals.

In addition to task-based activation analysis, resting-state fMRI revealed increased connectivity between the VWFA and left primary somatosensory cortex (S1) following training, alongside decreased connectivity between the VWFA and other visual areas. To further investigate the role of the VWFA in Braille reading, repetitive Transcranial Magnetic Stimulation (rTMS) was applied to the VWFA and two control structures (the lateral occipital area and the vertex). During rTMS, participants performed a lexical decision task involving tactile Braille words and pseudowords. Following VWFA stimulation, a statistically significant decrease in Braille reading accuracy was observed, underscoring the VWFA's critical involvement in tactile reading.

A separate study by the same research team examined the impact of tactile Braille learning on structural neuroplasticity in both grey and white matter (Bola, Siuda-Krzywicka, et al., 2017).

Whole-brain analysis revealed significant increases in the volume of the early visual cortex, left cerebellum, and premotor cortex, changes specific to Braille reading, as no similar results were observed in passive control subjects. A region of interest (ROI) analysis further confirmed that tactile Braille training-induced reorganisation within the peripheral early visual cortex.

White matter connectivity, assessed using diffusion tensor imaging, showed changes consistent with those observed in grey matter. An increase in fractional anisotropy (FA) was reported in the peripheral left early visual cortex. Additionally, positive changes in FA were noted in the frontal lobes and perisylvian regions of the right hemisphere. An ROI analysis of white matter demonstrated that the FA changes in the peripheral early visual cortex were specific to Braille reading. This area, typically active in non-visual tasks, is engaged in Braille reading, memory, and language in blind individuals (Amedi et al., 2003; Bedny et al., 2011; Raz et al., 2005), and sighted individuals after blindfolding and tactile training, it is active in Braille letter recognition (Merabet et al., 2008).

However, several limitations of the study should be noted. With only two time points, nine months apart, the study does not provide detailed information on the dynamics of the reported changes. While some functional changes occurred after months of learning, others may have emerged within weeks or even days. Additionally, although the LDT used in this study identified reading-specific activations during both tactile and visual Braille reading, the authors did not compare these modalities to identify regions more involved in linguistic processing during tactile reading than visual reading.

The most recent experiment tracked the dynamics of structural and functional changes during Braille learning (Matuszewski et al., 2021). Unlike previous studies, this research involved five MRI scanning sessions: before the course began, after 2.5, 5, and 8 months of learning, and following a 2.5-month break. The 8-month course, described in detail in a separate publication (Bola et al., 2016), primarily involved self-paced work using an A4 training card each day. During the first two months, participants met with a Braille instructor twice per month; after that, meetings were held monthly in small groups. The course introduced 16 Polish letters and focused initially on mastering tactile reading techniques and shape recognition.

An extended version of the general linear model (GLM) was employed, enabling a multimodal analysis of both structural (grey matter volume and longitudinal relaxation rate) and functional neuroplasticity associated with tactile Braille learning. After 8 months,

cumulative training effects were observed bilaterally in the visual cortex, motor cortex, premotor cortex, somatosensory cortex, superior frontal gyrus, middle frontal gyrus, and inferior frontal gyrus. Changes were also noted in the left hemisphere's lingual gyrus.

For each modality, follow-up analyses revealed functional changes in the motor cortex, somatosensory cortex, inferior frontal gyrus, thalamus, superior parietal cortex, and cerebellum bilaterally after 8 months. In the left hemisphere, increased activation was observed in the VWFA. Structural reorganisation related to myelin was detected bilaterally in the middle frontal gyrus and superior temporal gyrus in the right hemisphere, and in the VWFA. Grey matter volume increased bilaterally in the cuneus and superior occipital gyrus, and, in the right hemisphere, also increased in the early visual cortex, precentral, and postcentral gyri.

A separate analysis of white matter architecture (Molendowska et al., 2021) demonstrated a significant increase in fractional anisotropy (FA) after 8 months of learning tactile reading, specifically in the left hemisphere's postcentral and middle occipital gyrus. After a 3-month break from learning, FA levels in these structures returned to baseline, as measured at the beginning of the course.

Notably, functional changes were detected more rapidly than structural changes. After approximately 3 months of learning, significant increases in activity during tactile reading were observed bilaterally in the inferior frontal gyrus, thalamus, and caudate. The postcentral gyrus, middle frontal gyrus, and cerebellum became more active in the right hemisphere. In contrast, in the left hemisphere, increased activity was noted in the precentral gyrus, superior parietal lobule, superior frontal gyrus, inferior temporal gyrus, and inferior parietal lobule.

These findings demonstrate that cross-modal neuroplasticity resulting from learning can manifest in structure and function with different reorganisation patterns. Consistent with previous studies, regions involved in sensory information processing and higher-order cognitive functions become active during tactile reading. Additionally, areas of the visual reading network, such as Broca's area and the VWFA, begin responding to tactile reading within the first 3 months of learning.

The reviewed Braille studies have significantly contributed to understanding how Braille learning influences cross-modal plasticity. Braille reading activates motor and sensory regions as well as the brain's reading network. Notably, the VWFA is engaged during tactile reading, indicating that this area does not require visual input to be active. However, there are

several areas where further research could deepen our understanding of cross-modal plasticity.

First, there is a need for studies that utilise complex tasks with both linguistic and somatosensory components, such as the LDT, within the first three months of learning. Since neuroplasticity can manifest within weeks, days, or even minutes, examining the early stages of functional reorganisation during Braille learning may provide additional insights.

Second, comparing visual and tactile LDTs could help identify specific regions of the reading network that are uniquely engaged during tactile reading. This comparison has not yet been explored and could reveal critical insights into modality-specific processing.

Finally, a direct comparison between sighted Braille learners at the peak of their skill and blind Braille experts is necessary. Such a study could illuminate the similarities and differences in cross-modal plasticity between individuals with and without sensory deficits, providing a more nuanced understanding of the phenomenon. The primary target of inference in this dissertation is the adult reading network, particularly the left IFG and the left ventral occipitotemporal cortex, including the VWFA region. Neuroplasticity is the mechanism under study, and Braille learning is the experimental model used to test how that network adapts to a novel sensory channel.

2. ORIGINAL RESEARCH RATIONALE

Braille reading offers a unique opportunity to study cross-modal plasticity, a remarkable adaptive feature of the brain where the loss or alteration of one sensory modality induces cortical reorganisation, enhancing sensory performance in the remaining modalities. Braille training engages basic motor and sensory regions and brain areas associated with higher-order cognitive functions, providing a comprehensive model to study cross-modal plasticity (Matuszewski et al., 2021). Importantly, cross-modal plasticity is not limited to individuals with sensory impairments. For instance, when blindfolded, sighted adults also show increased activation in the early visual cortex during tactile stimulus discrimination (Merabet et al., 2008). More recent studies have provided valuable insights into the dynamics of training-induced plasticity, including cross-modal plasticity through Braille reading in sighted individuals (Matuszewski et al., 2021; Siuda-Krzywicka et al., 2016). These studies collectively indicate that tactile reading stimulates motor and sensory regions, the reading network, and brain areas linked with advanced cognitive functions, such as the VWFA. Notably, the first effects were observed after three months of training. However, given that neuroplasticity can manifest within weeks (Debowska et al., 2016), days (Chen et al., 2019), or even minutes (Sagi et al., 2012), the temporal dynamics of functional reorganisation during the early stages of Braille learning should also be examined. So far, no study has leveraged a linguistic task to observe activation shifts within the first few weeks of Braille learning. Additionally, previous research with sighted Braille learners has focused mainly on explicit reading or on simple tactile pattern-recognition tasks. However, in everyday life, much of the interaction between sighted individuals and reading occurs without conscious effort, for example, when reading a book or subtitles while watching a movie. This form of reading can be defined as implicit (Ross & Kowler, 2013).

2.1. Dissertation aims, research questions, and chapter roadmap

Braille learning in sighted adults provides a unique controlled model for testing how the adult reading network adapts to a novel route of orthographic input. The primary aim of this dissertation is therefore not simply to describe neuroplasticity in general, but to use Braille learning and Braille reading to investigate whether reading-related processing in adulthood recruits a shared core network across visual and tactile input while also preserving modality-, task-, and experience-dependent differences in its broader implementation.

In this dissertation, modality refers primarily to the sensory route through which orthographic input is processed, with the key contrast being between visually presented and tactually presented orthography. At the same time, the comparison between print and visual Braille also captures differences in orthographic format within the visual modality. The term metamodal is used here in a restricted sense to refer to shared recruitment of reading-related brain regions across input routes and formats; it does not imply identical computations, complete modality independence, or insensitivity to sensory experience.

This dissertation addresses four main research questions.

1. Longitudinal plasticity during Braille acquisition.

Does Braille training in sighted adults induce behavioural and functional changes beyond simple task repetition, and what is the temporal profile of those changes across tactile and visual Braille reading?

2. Shared versus condition-specific reading networks.

Which components of the reading network are shared across print, visual Braille, and tactile Braille, and which are more specific to Braille or to a particular input route?

3. Automatic reading-relevant engagement during a non-linguistic tactile task.

Does Braille learning lead to stronger recruitment of reading-relevant and associated sensorimotor-attentional networks during a 6-dot detection task that does not explicitly require reading?

4. The role of sensory experience in tactile reading.

Which aspects of explicit and implicit Braille processing are shared between sighted Braille learners and congenitally blind proficient Braille readers, and which differ as a function of sensory experience, expertise, and task demands?

The main predictions were as follows. First, longitudinal Braille learning was expected to lead to behavioural improvement. It increased task-related brain activation during tactile and visual Braille reading, relative to the pre-training baseline, particularly in reading-related and sensorimotor regions. In contrast, no comparable change was expected between the two pre-training sessions or during print reading. Second, print, visual Braille, and tactile Braille were expected to share a left-lateralised reading-related core, particularly in inferior frontal and ventral occipitotemporal cortex, alongside additional sensory, sensorimotor, parietal, cerebellar, and subcortical recruitment that would differ across conditions. Third, Braille

learners were expected to show stronger activation than passive controls in reading-relevant and sensorimotor-attentional regions during the 6-dot detection task, although these effects were not assumed to reflect process-pure implicit reading. Fourth, sighted learners and blind Braille readers were expected to show partial overlap in higher-level tactile reading, alongside stronger occipital involvement in blind readers and stronger frontoparietal-sensorimotor scaffolding in sighted learners. The empirical part of the dissertation consists of four studies corresponding to the four research questions above. Chapter 4 examines longitudinal behavioural and functional changes during tactile and visual Braille acquisition in sighted adults. Chapter 5 identifies shared and modality-specific components of the reading network across print, visual Braille, and tactile Braille. Chapter 6 tests whether Braille learning leads to automatic reading-relevant engagement during a non-linguistic tactile 6-dot detection task. Chapter 7 compares tactile Braille processing in sighted learners and congenitally blind proficient readers. Chapter 8 integrates these findings and discusses their theoretical implications and limitations.

3. Methods and materials

3.1. Participants

3.1.1. Experimental group

Twenty-one right-handed females began the study. Two participants took part in the braille course but resigned before it ended. One participant left due to health-related problems before learning began, and another left the study before the follow-up session, resulting in a final number of 17 participants. We collected informed consent before the study. The Committee for Research Ethics of the Institute of Psychology of the Jagiellonian University approved this study. We selected all participants from among candidates who completed an online questionnaire focused on demographics, education and general linguistic and health-related issues. The current study was one of two arms in a project investigating experience-related neuroplasticity, with the other arm using musical training instead of Braille reading training. To ensure participant uniformity, we included questions about musical education and experience in the recruitment questionnaire. Our final inclusion criteria were as follows: a) female, b) native Polish language speakers, c) university students, d) no prior experience with the Braille reading system, and e) no factors precluding the possibility of participating in MRI scans. For practical purposes, we recruited only students from a pedagogical university (Grzegorzewska University) in the experimental group. This is one of the very few schools offering a degree in typhlopedagogy - a branch of pedagogy dealing with the education of the visually impaired. As a result, we were more likely to find motivated candidates here than anywhere else. Before the study commenced, we collected informed consent. At every time point, we conducted MRI safety screenings. None of the subjects had previously participated in any studies on brain plasticity published by members of our research group.

3.1.2. Control group

We also recruited 21 right-handed females to participate as a passive control group in the study. Two participants resigned from the study. The final sample, therefore, consists of 19 participants. Our control group recruitment criteria were the same as those for the experimental group, though we did not restrict recruitment to the pedagogical school. Furthermore, we matched controls demographically to the experimental group and found no statistically significant differences in the key demographic variables. **Table 2** shows the results of the mentioned analyses:

Table 2. Statistical comparison of demographic variables between experimental and control groups.

<i>Variable</i>	<i>Group</i>	<i>M</i>	<i>SD</i>	<i>t</i>	<i>df</i>	<i>p</i>	<i>d</i>
Age	Experimental	21.00	1.37	- 0.33	34.77	0.75	- 0.11
	Control	20.84	1.57				
Number of foreign languages known	Experimental	2.28	1.02	- 0.59	30.90	0.56	- 0.19
	Control	2.11	0.74				

Note. *M* = mean, *SD* = standard deviation, *t* = Student's t-test result, *df* = degrees of freedom, *p* = level of significance, *d* = Cohen's d effect size.

3.1.3. Blind group

In addition to experimental and passive control groups, we invited 21 blind people (14 female, 7 male) to participate in a single experimental session (age range: 23-49; *M* = 34.76, *SD* = 6.87). Because it is difficult to recruit such people, we decided not to restrict recruitment to females but to the blind population in general.

3.2. Experimental design

During the study, the subjects in the experimental group took part in seven behavioural and neuroimaging sessions: two pre-exposure (time point -1; *TP*₋₁ and *TP*₀), three during (*TP*₁ - *TP*₃), one at the end (*TP*₄) and one three months after the end of training (*TP*₅) (See **Figure 1** below). During each session, we acquired behavioural and neuroimaging data. The control participants did not take part in the first pre-exposure session (*TP*₋₁). The blind group was invited for a single experimental session (*TP*₄).

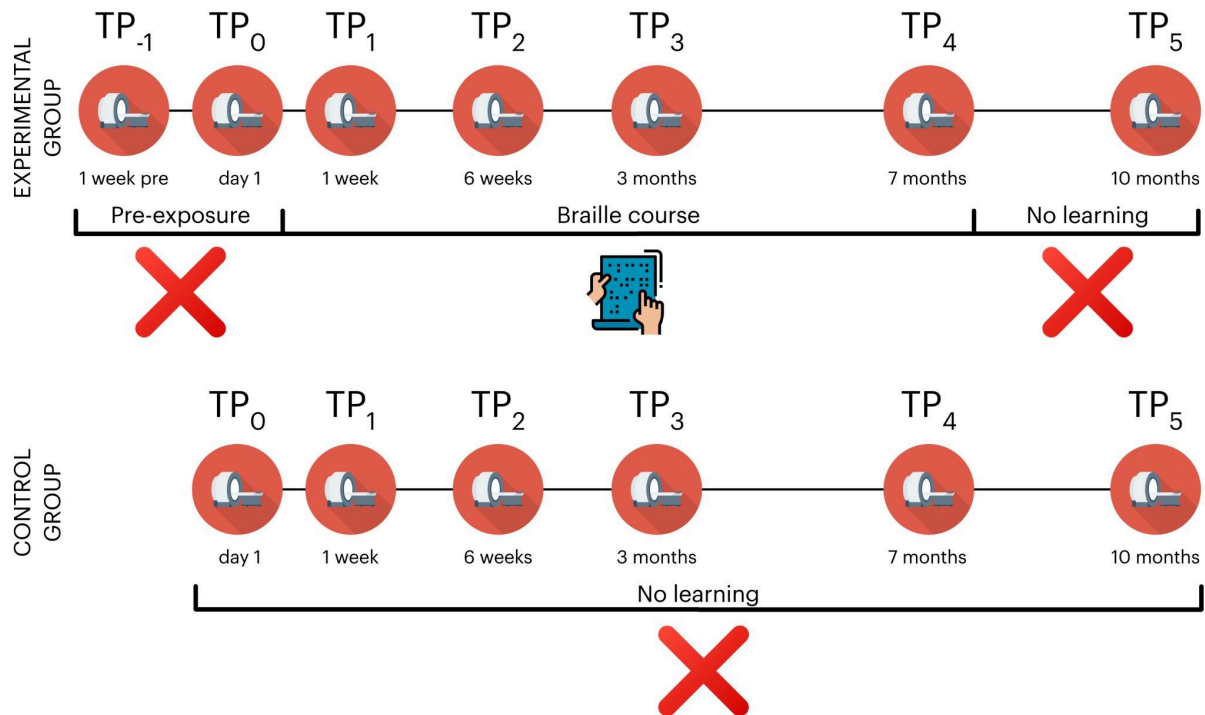


Figure 1. Overview of experimental design in the Braille learning (experimental) and passive control groups. The control group did not participate in TP₋₁ (a pre-scan a week before the beginning of the course).

3.3. Braille course

The Braille tactile reading course was scheduled for six months. Due to the ongoing pandemic and the lack of means of conducting on-site research, we extended the course duration to seven months. The course consisted of nine online meetings with an instructor and asynchronous work by all participants, utilising six sets of Braille study cards. The first month of study included 60 cards per set, while subsequent months had 30 cards per set. In the last month of training, cards from previous months were used. For each study card, the workload was estimated from ten to twenty minutes of tactile reading - approximately a total of 52.5 hours of self-practising without any repetition. The first three meetings on the first, seventh and fourteenth day were held in small groups of no more than five students. All the other meetings were held in larger groups of around ten students. We delivered the asynchronous course together with a set of instructions. The instructions for the first month were the strictest. In the first week, the participants received a list of individual tasks that had to be completed on a specific day of the course. The remaining weeks of the first month were organised in a weekly manner. The instructions for months 2-6 were not organised in any timely manner - the participants were free to learn and process the material at their own pace, though they were highly encouraged to complete one card per day. The instructions in month

7 focused on reviewing the entire course material. The course focused primarily on teaching Braille reading in the tactile domain. At the same time, the participants had to learn the Braille alphabet visually to verify if they had resolved the tasks correctly.

In line with previous Braille courses (Bola et al., 2016; Matuszewski et al., 2021), the current course covered 16 Braille letters of the Polish alphabet - A, B, C, D, E, I, K, L, Ł, M, O, P, S, T, U, Y. Importantly those letters were the core material tested in the MRI experimental sessions.

The first week of the course was the most demanding. The participants had to learn the proper way of moving their hands through the Braille card or shape discrimination during the meetings and later on their own. They were instructed to read with their right index fingers and to navigate the Braille card with their left index fingers. At the same time, the instructor introduced the first eight most straightforward letters (A, B, C, D, E, K, L, O). During weeks 2-5, four new letters (I, M, S, T) were introduced. During weeks 6-12, the participants were presented with the remaining core letters (Ł, P, U, Y). While months 4-6 of the course focused on mastering the core letters, they also introduced new material to maintain high interest and engagement. The fourth month of the course introduced two new signs - a Braille dot and a sign indicating an uppercase letter. The fifth month of the course introduced six new letters of the Polish alphabet (Ą, Ę, F, G, J, N). The sixth month of the course introduced the remaining ten letters (Ć, H, Ń, Ó, R, Ś, W, Z, Ż, Ż) (**Figure 2**).

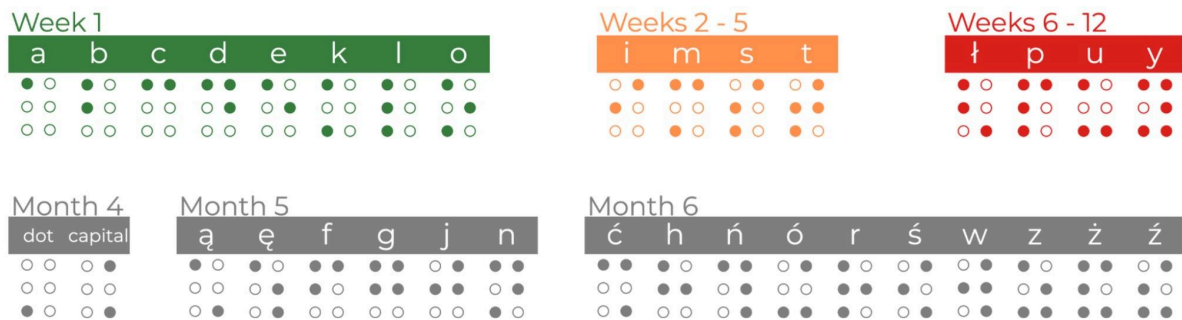


Figure 2. The overview of the learning material during the Braille course. The core letters (coloured in green, orange and red) were A, B, C, D, E, I, K, L, Ł, M, O, P, S, T, U and Y. During the course, additional letters were introduced: Ą, ć, ę, f, g, h, j, n, ń, ó, r, ś, w, z, ż, ź. The symbols of a dot and a capital letter were also introduced.

3.4. Statistical analysis of behavioural data

We used a repeated measures analysis of variance (rmANOVA) to analyse the Braille behavioural data. We conducted a one-way analysis with time as a factor for the online and on-site Braille reading tasks and a two-way analysis with time and condition as factors for the fMRI LDTs. All post-hoc tests - paired t-tests - were computed with Bonferroni correction for

multiple comparisons. Greenhouse-Geisser F-tests and degrees-of-freedom corrections were used for cases with violated sphericity.

3.5. Behavioural tests

3.5.1. Online Braille reading tests

We conducted six online tests to assess the participants' reading skills and maintain a high level of motivation throughout the course. The tests were conducted after four, nine, thirteen, eighteen, twenty and twenty-four weeks of learning.

Each test consisted of tactile and visual Braille letters and word reading. However, the first test was an exception to that rule, as we only tested tactile word reading at that time. In the tactile task, we asked the participants to blindfold themselves and read words from a selected Braille card. In the visual task, we asked the participants to read words presented on the screen. All the words in the visual task were based on the course material.

3.5.2. Onsite tests

On-site tests were conducted during participants' lab visits for MRI experimental sessions. As with the online tests, we assessed Braille reading skills in the visual and tactile domains. The participants were presented with two tasks: word reading and letter reading. Every word-reading test consisted of 15 words (3 to 5 letters long). Every letter-reading test consisted of 28 letters. We asked the participants to read aloud as many words (or letters) as possible in one minute. In all tasks, the stimuli were presented on printed sheets. In every experimental session, the words used in tests consisted only of those core letters already presented in the Braille course. We introduced a pseudo-randomised order of letters in the letters reading task, so the ones already shown in the course appeared before all the other letters. The outcome was the number of letters or words the participant read correctly in one minute.

3.5.3. Cognitive tasks

On three separate occasions: TP₀ (day one), TP₄ (seven months) and TP₅ (follow-up), the participants from both experimental and control groups performed a series of cognitive tasks to test if any potential far transfer occurred explicitly due to Braille learning. None should be expected, considering the most recent studies on this matter (Nichols et al., 2021; Sala et al., 2019).

3.5.3.1. Stroop task

We conducted a Stroop test to assess the potential effect of Braille learning on the ability to inhibit cognitive interference (Stroop, 1935). We used a dedicated version of the task made

available online by the Presentation software designers (Neurobehavioral Systems, Inc.). The procedure consists of two conditions. In the first condition, the task was to name the colour in which the word was written. In the second condition, the task was to identify the colour spelt by the word (**Figure 3**).

	Congruent	Incongruent	Control
Naming the ink	red	blue	#####
Naming the spelled colour	green	yellow	blue

Figure 3. The conditions in the Stroop test.

3.5.3.2. N-back task

To assess the potential effect of Braille learning on working memory, we did two kinds of n-back tasks: musical and visual. The musical task data were collected as part of a larger project in our lab; we will not describe it here. The visual n-back task was done using letters on three levels of difficulty: 1-back, 2-back and 3-back. The participants were presented with a sequence of letters (one at a time), and whenever the presented letter matched the one n steps back, they were to press a button. The task was programmed using the Presentation software (Neurobehavioral Systems, Inc.). **Figure 4** shows examples of trials in all the variants of the task used.

1-back	2-back	3-back
A B <u>C</u> A <u>D</u> <u>D</u> B <u>C</u> <u>C</u>	D B A <u>C</u> A <u>D</u> B <u>D</u> <u>C</u> <u>D</u>	<u>A</u> B C A <u>D</u> B <u>A</u> C B A

Figure 4. Examples of a letter-based n-back task. In the 1-back task, participants had to react whenever the presented letter matched the one that appeared just before (one step back). The letters marked in red are the same as the letters one step earlier (underlined), and the participant should respond by pressing the button. The 2- and 3-back tasks were done analogically.

3.6. Neuroimaging sequences

We acquired the MRI data using a Siemens Trio 3T scanner with a 32-channel coil. We obtained a structural T1-weighted ($T1_w$) image using a standard MPRAGE sequence (Field of view (FoV): 256 x 256 mm, voxel size: 1 x 1 x 1 mm, repetition time (TR): 2530 ms, echo time (TE): 3.32 ms, inversion time (TI): 1100 ms, flip angle (FA): 7 degrees, number of slices: 176). The functional data were acquired using an Echo Planar Imaging pulse sequence (FoV: 672 x 656 mm, voxel size: 2.5 x 2.5 x 2.5 mm, TR: 1410 ms, TE: 30.4 ms, FA: 56 degrees).

3.7. fMRI tasks

3.7.1. Lexical Decision Tasks

In each experimental session, participants in the experimental group performed three types of LDTs in the MRI scanner in the following order: visual using the Polish alphabet, tactile using the Braille alphabet, and visual using the Braille alphabet. **Figure 5** outlines the steps of the three tasks:

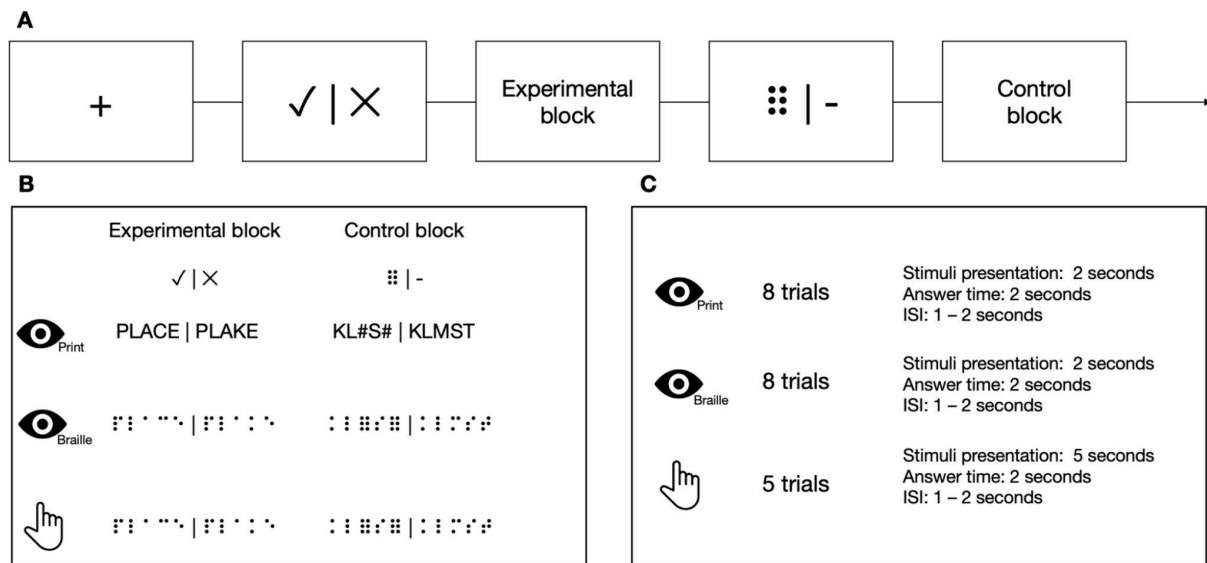
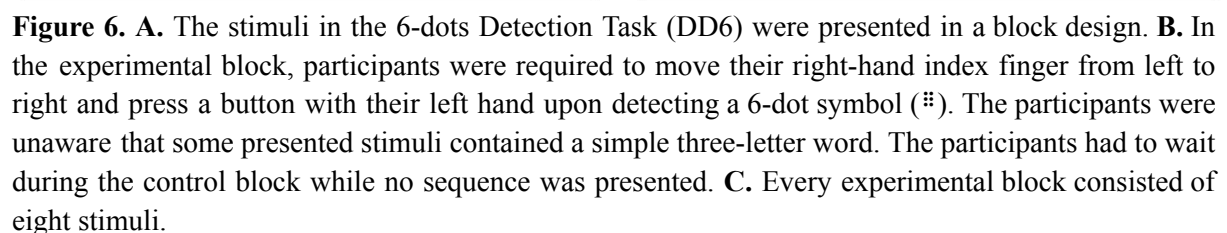


Figure 5. **A.** The stimuli in Lexical Decision Tasks were presented in a block design. **B.** In the experimental block, the participants had to decide whether the stimulus was a real word or a pseudoword. In the control block, the participants had to determine whether the presented stimulus contained two six-points (or hashtags in the print task). **C.** In visual tasks, each block consisted of eight stimuli. In the tactile task, each block consisted of five stimuli.

In the experimental block, the participants had to decide whether the presented sequence of letters constituted a real word or was just a set of letters that resembled one but, in reality, did

In Braille tasks, the words were drawn from the list of the most frequently used words in Polish (Mandera et al., 2015). The final stimuli were three to five letters long. The pseudowords were created by changing one letter in a word, keeping the presented stimulus similar to a real word while still not being one. Words and pseudowords were created only from letters already introduced in the course (the only exceptions to the rule were TP₋₁ and TP₀, the time points before the beginning of the course, which used the whole set of core letters presented in the core part of the course).

Participants in the experimental and control groups completed a Braille 6-dot Detection Task (DD6) in each experimental session. **Figure 6** outlines the steps in this task:



In the experimental block, the participants sequentially moved their right index finger from left to right and pressed a button whenever they detected the six-dot symbol (⠼).

The participants were not informed that approximately half of the stimuli in the experimental block consisted of short, three-letter words. We introduced the words to estimate the effect of implicit processing in people learning to read Braille. In the control block, there was no task; the participant rested. Each block was preceded by a fixation cross (in pseudo-randomised duration between 6 and 8 seconds) and a visual indication of the block to be presented (1 to 2 seconds). In the experimental condition, each block consisted of 8 stimuli, each presented for 5 seconds, with a 1-second ISI. In the control condition, each block consisted of two empty blocks, each presented for 5 seconds, and a 1-second ISI.

3.8. MRI data preprocessing

3.8.1. Anatomical data

A total of 7 T1-weighted (T1w) images were acquired per subject within the input BIDS dataset. All of them were corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.3.3 ((Avants et al., 2008), RRID: SCR_004757). The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as the target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white matter (WM) and grey matter (GM) was performed on the brain-extracted T1w using fast (FSL 6.0.5.1:57b01774, RRID: SCR_002823, (Zhang et al., 2001)). A T1w-reference map was computed after registration of 7 T1w images (after INU-correction) using mri_robust_template (FreeSurfer 6.0.1, (Reuter et al., 2010)). Volume-based spatial normalisation to two standard spaces (MNI152NLin2009cAsym, MNI152NLin6Asym) was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. The following templates were selected for spatial normalisation: ICBM 152 Nonlinear Asymmetrical template version 2009c ((Fonov et al., 2009), RRID: SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym), FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model [(Evans et al., 2012), RRID: SCR_002823; TemplateFlow ID: MNI152NLin6Asym].

3.8.2. Functional data

The following preprocessing was performed across all tasks for each functional session per subject. First, a reference volume and its skull-stripped version were generated by aligning and averaging 1 single-band reference (SBRef). Head-motion parameters with respect to the BOLD reference (transformation matrices and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using `mcfliirt` (FSL 6.0.5.1:57b01774, (Jenkinson et al., 2002)). Functional runs were slice-time corrected to 0.672s (0.5 of slice acquisition range 0s-1.34s) using `3dTshift` from AFNI ((Cox & Hyde, 1997), RRID: SCR_005927). The BOLD time series (including slice-timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head motion. These resampled BOLD time series will be called preprocessed BOLD in the original space or just preprocessed BOLD. The BOLD reference was then co-registered to the T1w reference using `mri_coreg` (FreeSurfer) followed by `flirt` (FSL 6.0.5.1:57b01774, (Jenkinson & Smith, 2001) with the boundary-based registration (Greve & Fischl, 2009) cost-function. Co-registration was configured with six degrees of freedom. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Several confounding time series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions (Power et al., 2014) and Jenkinson (relative root mean square displacement between affines, (Jenkinson et al., 2002)). FD and DVARS are calculated for each functional run using their Nipype implementations (following the definitions by (Power et al., 2014)). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, physiological regressors were extracted for component-based noise correction (CompCor, (Behzadi et al., 2007)). Principal components are estimated after high-pass filtering the preprocessed BOLD time series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that, instead of eroding the masks by 2 pixels on BOLD space, the aCompCor masks subtract a mask of pixels likely containing a volume fraction of GM. This mask is obtained by thresholding the corresponding partial volume map at 0.05, and it ensures components are not extracted from

voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarised by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 per cent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded by including temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers. The BOLD time series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Automatic removal of motion artefacts using independent component analysis (ICA-AROMA (Pruim et al., 2015)) was performed on the preprocessed BOLD on MNI space time-series after removal of non-steady state volumes and spatial smoothing with an isotropic Gaussian kernel of 6mm FWHM (full-width half-maximum). Corresponding “non-aggressively” denoised runs were produced after such smoothing. The “aggressive” noise regressors were also collected and placed in the corresponding confounds file. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using `antsApplyTransforms` (ANTs), configured with Lanczos interpolation to minimise the smoothing effects of other kernels ((Lanczos, 1964)). Non-gridded (surface) resamplings were performed using `mri_vol2surf` (FreeSurfer).

Many internal operations of fMRIPrep use Nilearn 0.8.1 ((Abraham et al., 2014), RRID: SCR_001362), mainly within the functional processing workflow. For more details on the pipeline, see the workflow section in fMRIPrep's documentation.

3.9. Functional data: Statistical analyses

3.9.1. Subject level

3.9.1.1. Lexical Decision Tasks

First, functional data from three LDTs (print in Polish (L1), visual Braille and tactile Braille) in the experimental group were analysed using a GLM at the subject level. The timings of the experimental and control blocks were entered separately at each time point, along with six head-movement regressors. The haemodynamic response was modelled using the default functions of SPM 12.7771. All data were filtered with a 128s high-pass filter. For each subject, for every task and at every time point, the *experimental* > *control* contrast was computed. Each contrast was also masked using the brain mask from the fMRIPrep preprocessing pipeline.

In the blind group, the functional data of the tactile Braille LDT were analysed using a GLM at the subject level. The timings of experimental and control blocks were entered together with six head movement regressors. The haemodynamic response was modelled using the default functions of SPM 12.7771. All data were filtered with a 128s high-pass filter. For each subject, the *experimental* > *control* contrast was computed. Each contrast was also masked using the brain mask from the fMRIPrep preprocessing pipeline.

3.9.1.2. 6-Dots Detection Task

In the DD6 task, the functional data of the experimental and control groups were analysed using a GLM at the subject level. The timings of the experimental and control blocks were entered separately at each time point, along with six head-movement regressors. The haemodynamic response was modelled using the default functions of SPM 12.7771. All data were filtered with a 128s high-pass filter. The experimental contrast was computed for each subject at every time point. Each contrast was also masked using the brain mask from the fMRIPrep preprocessing pipeline.

In the blind group, the functional data were analysed using a GLM at the subject level. The timings of experimental and control blocks were entered together with six head movement regressors. The haemodynamic response was modelled using the default functions of SPM 12.7771. All data were filtered with a 128s high-pass filter. For each subject, the *experimental* contrast was computed. Each contrast was also masked using the brain mask from the fMRIPrep preprocessing pipeline.

3.9.2. Group level

3.9.2.1. Longitudinal Braille acquisition in sighted adults

On the group level, the GLMs were specified using SPM12's flexible factorial model.

Task repetition effect analysis

To test for the repetition effect, the data were analysed in three separate models:

1. Print LDT model comparing two time points before the course (TP_{-1} and TP_0);
2. Visual Braille LDT model comparing two time points before the course (TP_{-1} and TP_0).
3. Tactile Braille LDT model comparing two time points before the course (TP_{-1} and TP_0).

We performed two comparisons for every model: $TP_{-1} > TP_0$ and $TP_0 > TP_{-1}$. All contrasts were masked with an anatomical mask to exclude voxels of no interest. Additionally, the results were thresholded at the voxel level using a Family-Wise Error (FWE) correction, with a p -value of 0.05 and a cluster extent of 20 voxels.

Main effects and pairwise comparisons

To investigate the effects of Braille learning, the data were analysed in three additional models:

1. Print LDT model comparing six time points throughout the course ($TP_0 - TP_5$);
2. Visual Braille LDT model comparing six time points throughout the course ($TP_0 - TP_5$).
3. Tactile Braille LDT model comparing six time points throughout the course ($TP_0 - TP_5$).

In each LDT model, a 6×1 rmANOVA was performed with time point as a factor. Additionally, a series of pairwise comparisons between time points was conducted to explore the effects of Braille learning. Every comparison was masked using results from the main effect of time, retaining only voxels that showed significant changes in activity over the course. Additionally, the results were thresholded at the voxel level using FWE correction with a p -value of 0.05 and a cluster extent of 20 voxels. All analyses were masked with an anatomical mask to exclude voxels of no interest.

3.9.2.2. Shared and modality-specific reading networks in print and Braille

To look for regions that constitute parts of sensory-dependent and independent networks involved in language processing, a single GLM was specified using SPM12's flexible factorial model. A 3 x 1 rmANOVA was performed with the task as a factor. Each task was represented by the main effect of condition (experimental > control), which pooled data from six time points collected throughout the course (TP₀-TP₅). All results were thresholded at the voxel level using FWE correction, with a *p*-value of 0.05 and a cluster extent of 20 voxels. All analyses were masked with an anatomical mask to exclude voxels of no interest.

Sensory independent networks' analysis

To investigate which regions can be considered sensory-independent and engaged in the reading process regardless of the modality of the lexical stimuli, a conjunction analysis was performed by looking for voxels engaged in all three LDTs.

Braille-general activations

To investigate which regions can be considered sensory-independent but engaged specifically in the Braille reading process, regardless of the modality of the lexical stimuli, a conjunction analysis was performed by looking for voxels engaged in tactile and visual Braille LDTs. Voxels specific to Braille reading were extracted by excluding any active voxels in the main effect of the condition contrast of the print LDT.

Tactile Braille-specific activations

To investigate which regions can be considered sensory-dependent and specifically engaged in the tactile Braille reading process, an analysis was performed by identifying voxels activated during tactile Braille LDT. Any voxels showing engagement during the visual reading (print or Braille) were extracted by excluding any active voxels in the main effect of condition contrast of the print and visual Braille LDTs.

Visual Braille-specific activations

To investigate which regions can be considered sensory-dependent and specifically engaged in the visual Braille reading process, an analysis was performed by identifying voxels activated during visual Braille LDT. Any voxels showing engagement during the tactile Braille reading or visual reading (print) were extracted by excluding any active voxels in the main effect of condition contrast of the print and tactile Braille LDTs.

3.9.2.3. Automatic tactile reading-related engagement in Braille learners

In the DD6 task, the GLM was specified using SPM12's flexible factorial model. A 6 x 2 mixed ANOVA was performed with time point (TP₀ - TP₅) as a within-subject factor and group (experimental and control) as a between-subject factor. Additionally, pairwise comparisons between groups were conducted at each time point to examine differences in implicit reading processing between the learning and naive groups. Every comparison was masked using results from the main effect of time, retaining only voxels that showed significant changes in activity over the course. Additionally, the results were thresholded at the voxel level using an FWE correction with a *p*-value of 0.05 and a cluster extent of 20 voxels. All analyses were masked with an anatomical grey matter mask to exclude voxels of no interest.

3.9.2.4. Braille processing in sighted learners and blind readers

Tactile Braille Lexical Decision Task

To look for similarities and differences in brain activity between sighted and blind Braille readers, a single GLM was specified using SPM12's flexible factorial model. A 2 x 1 ANOVA was performed with the group as a factor. For the blind group, the data from the sole experimental session they attended was used. The end-of-learning (TP₄) data were used for the sighted learning group. All results were thresholded at the cluster level using an FWE correction and a *p*-value of 0.001.

6-Dots Detection task

In the DD6 task, the GLM was specified using SPM12's flexible factorial model. A 2 x 1 ANOVA was performed with the group as a factor. For the blind group, the data from the sole experimental session they attended was used. The data from the end of learning (TP₄) was used for the sighted learning group. All results were thresholded at the cluster level using an FWE correction and a *p*-value of 0.001.

EMPIRICAL STUDIES

4. Longitudinal Braille acquisition in sighted adults

How does the adult human brain adapt to new experiences? Would such an experience be processed differently by the brain when introduced by touch than by vision? Is it possible to observe a pattern of functional reorganisation in the brain throughout the intensive learning process, which incorporates vision and touch? How fast does the brain begin to adapt to such a process? Is the change consistent throughout the brain, or are there differences between the sensory systems and the higher-order associative areas?

Learning to read the Braille alphabet using touch is a highly specific yet excellent example of a complex skill that can be learned and controlled in a longitudinal scientific setting. The task is more cognitively demanding than visual language learning, as it involves reading letters and combining them into words through touch rather than vision. We already know that learning Braille tactile leads to functional neuroplasticity in multiple brain areas. They include somatosensory and visual language-processing areas, such as the VWFA (Debowska et al., 2016; Siuda-Krzywicka et al., 2016). It also impacts a structural change in the early visual cortex (Bola, Siuda-Krzywicka, et al., 2017). Unlike previous studies, the most recent Braille-related longitudinal study employed a complex model with multiple time points (Matuszewski et al., 2021). Such a setup allowed tracking the temporal dynamics in structural and functional neuroplasticity. The study has shown that while structural and functional changes occur, the brain's functional response is much more rapid, emerging within the first three months of learning across multiple language network areas (Dehaene, 2010), including, but not limited to, the VWFA. No Braille study has focused on neuroplasticity in the first three months of learning. However, other studies have suggested that the first functional neuroplastic changes associated with language learning occur within 3 months (Banaszkiewicz et al., 2021; Barbeau et al., 2017). Even the structural changes that typically occur following changes in brain function (Matuszewski et al., 2021; Molendowska et al., 2021) can emerge within days of learning (Vukovic et al., 2021). Outside of the language scope, learning novel motor skills can induce a functional change in the motor cortex after just an hour of learning (Arima et al., 2011). We took a unique, longitudinal experimental approach to examine the temporal dynamics of functional neuroplasticity during Braille learning. A group of sighted volunteers participated in a 10-month study that included 7 months of a Braille reading course. During the study, we invited them to join in 7 experimental sessions, which included functional and structural MRI procedures and

behavioural assessment of Braille reading skills and general cognition. We used tactile and visual Braille LDTs (Matuszewski et al., 2021) to assess functional brain plasticity associated with Braille reading.

4.1. Aims, research questions, and predictions

This longitudinal study was designed to examine how the adult reading network changes during Braille acquisition in sighted adults, while distinguishing learning-related plasticity from simple task repetition. The study focused on tactile and visual Braille lexical decisions, with print reading serving as an additional control task.

It addressed the following research questions:

1. Does Braille training lead to behavioural improvement and learning-related increases in task-related brain activity during tactile and visual Braille reading, beyond any repetition effects observed before training?
2. What is the temporal profile of these changes across early, intermediate, late, and follow-up sessions?
3. Do the left inferior frontal gyrus and left ventral occipitotemporal cortex become increasingly engaged during Braille learning, and do their time courses differ between tactile and visual Braille?
4. Are any training-related behavioural and neural changes retained after a three-month break in practice?

The main predictions were as follows. First, no significant repetition-related changes were expected between the two pre-training sessions, and no systematic longitudinal change was expected for print reading. Second, both Braille tasks were expected to show learning-related increases relative to baseline. Third, early training was expected to recruit frontoparietal, sensorimotor, and inferior frontal regions, with ventral occipitotemporal recruitment expected to emerge as Braille became more behaviourally meaningful. Finally, behavioural gains and at least part of the functional reorganisation were expected to remain detectable at follow-up, even if some attenuation occurred after the practice break.

4.2. Results

4.2.1. Behavioural results

4.2.1.1. On-site Braille reading tests

Visual Braille letters reading task

We computed a one-way rmANOVA on Braille reading letters per minute in the visual domain. We observe a statistically significant main effect of time, $F(6, 96) = 263.43$; $p < 0.001$; $\eta_p^2 = 0.94$. **Table 3** shows Bonferroni-corrected post-hoc comparisons between all the time points:

Table 3. Post-hoc comparisons between time points in the visual letters per minute reading task.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	0.47	0.87						
TP ₀	0.35	0.61	1					
TP ₁	9.76	4.10	< 0.001	< 0.001				
TP ₂	15.88	3.37	< 0.001	< 0.001	< 0.001			
TP ₃	17.82	2.98	< 0.001	< 0.001	< 0.001	1		
TP ₄	25.71	2.71	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
TP ₅	21.82	2.94	< 0.001	< 0.001	< 0.001	0.001	0.053	< 0.001

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *M* = Mean, *SD* = Standard deviation. *p* values with Bonferroni correction for multiple comparisons.

Post-hoc tests showed statistically significant differences between all the time points except for TP₋₁ and TP₀, TP₂ and TP₃, and TP₃ and TP₅.

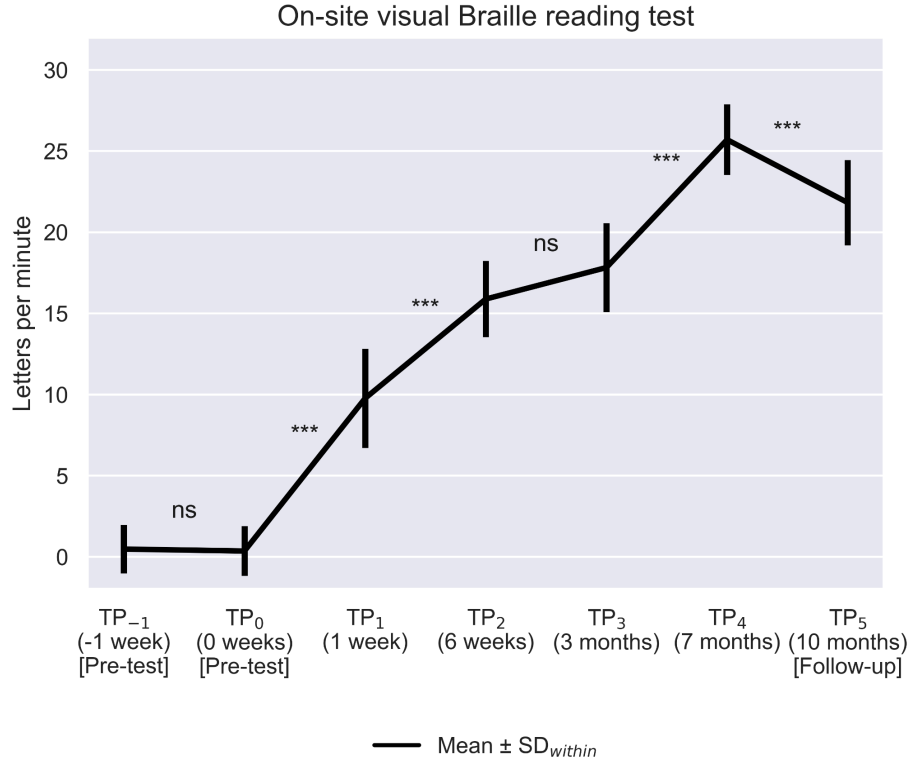


Figure 7. Visual Braille letters reading speed during training. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. TP = time point, **** - $p < 0.0001$, *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

As **Figure 7** shows, we see a systematic increase in visual letter reading throughout the course (TP₁ - TP₄). After a 3-month break from learning (TP₅), we observe a statistically significant decrease in letter reading per minute, indicating that participants performed worse than at TP₄.

Tactile Braille letters reading task

We computed a one-way rmANOVA on Braille reading letters per minute in the tactile domain. We observe a statistically significant main effect of time, $F(6, 96) = 153.53$; $p < 0.001$; $\eta_p^2 = 0.91$. **Table 4** shows Bonferroni-corrected post-hoc comparisons between all the time points:

Table 4. Post-hoc comparisons between time points in the tactile letters per minute reading task.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	0.12	0.33						
TP ₀	0.35	0.61	1					
TP ₁	6.53	2.60	< 0.001	< 0.001				
TP ₂	11.53	2.92	< 0.001	< 0.001	< 0.001			
TP ₃	14.82	2.32	< 0.001	< 0.001	< 0.001	0.01		
TP ₄	17.12	3.95	< 0.001	< 0.001	< 0.001	< 0.001	0.54	
TP ₅	14.59	3.45	< 0.001	< 0.001	< 0.001	0.11	1	0.38

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *M* = Mean, *SD* = Standard deviation. *p* values with Bonferroni correction for multiple comparisons.

Post-hoc tests showed statistically significant differences between all the time points, except for TP₋₁ and TP₀, TP₂ and TP₅, TP₃ and TP₄, TP₃ and TP₅, and TP₄ and TP₅ (**Figure 8**).

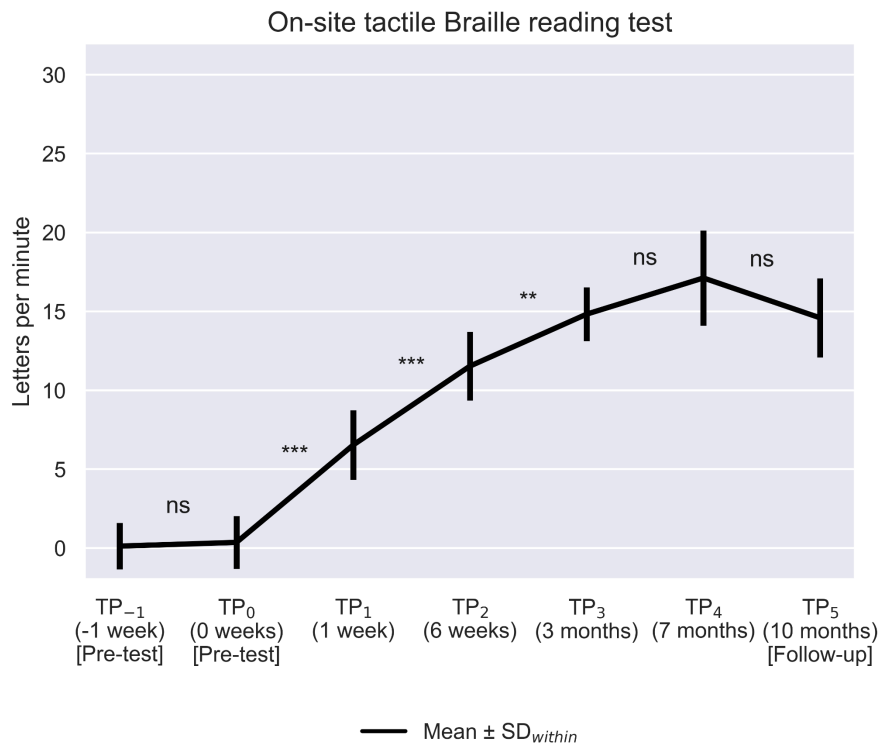


Figure 8. Tactile letters reading speed during training. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

Visual Braille words reading task

We performed a one-way rmANOVA to examine Braille reading words per minute) in the visual domain. We observe a statistically significant main effect of time, $F(6, 96) = 115.43$; p

< 0.001 ; $\eta_p^2 = 0.88$. **Table 5** shows Bonferroni-corrected post-hoc comparisons between all the time points:

Table 5. Post-hoc comparisons between time points in the visual words per minute reading task.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	0.00	0.00						
TP ₀	0.00	0.00	1					
TP ₁	7.82	4.11	< 0.001	< 0.001				
TP ₂	10.12	3.52	< 0.001	< 0.001	1			
TP ₃	13.59	1.91	< 0.001	< 0.001	0.001	0.004		
TP ₄	14.41	0.87	< 0.001	< 0.001	< 0.001	0.001	1	
TP ₅	11.65	3.44	< 0.001	< 0.001	0.03	1	0.18	0.12

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *p* values with Bonferroni correction for multiple comparisons. No *p*-value was calculated for the TP₋₁ and TP₀ comparison due to a lack of variability in the results; we imputed a *p*-value of 1.

Post-hoc tests showed statistically significant differences between all the time points, except for TP₋₁ and TP₀, TP₁ and TP₂, TP₂ and TP₅, TP₃ and TP₄, TP₃ and TP₅, and TP₄ and TP₅ (**Figure 9**).

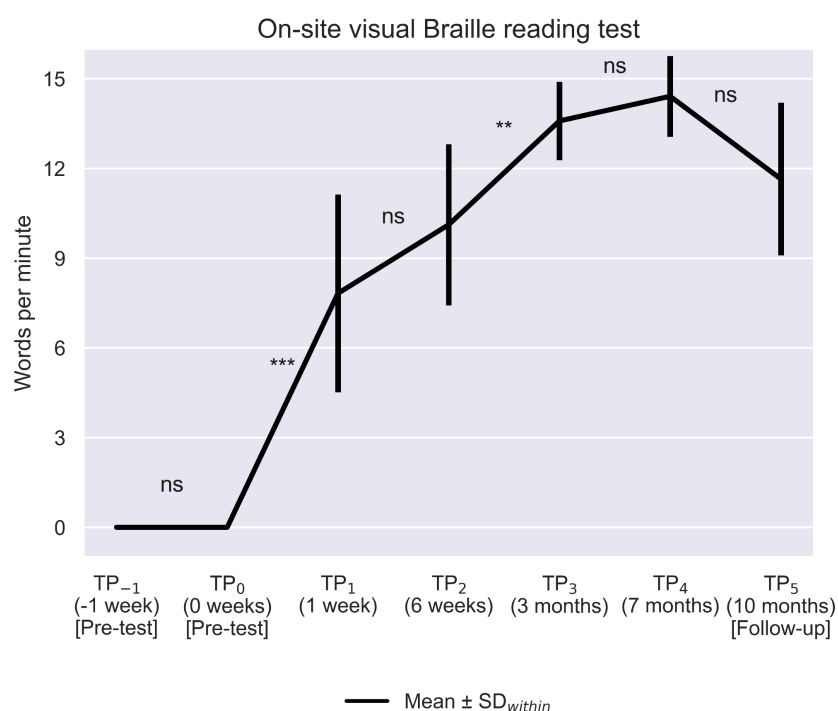


Figure 9. Visual Braille words reading speed during training. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

Tactile Braille words reading task

We computed a one-way rmANOVA on Braille reading words per minute in the tactile domain. We observe a statistically significant main effect of time, $F(6, 96) = 23.61$; $p < 0.001$; $\eta_p^2 = 0.60$. **Table 6** shows Bonferroni-corrected post-hoc comparisons between all the time points:

Table 6. Post-hoc comparisons between time points in the tactile words per minute reading task.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	0.00	0.00						
TP ₀	0.00	0.00	1					
TP ₁	2.76	2.95	0.03	0.03				
TP ₂	1.94	1.85	0.01	0.01	1			
TP ₃	6.12	4.55	0.001	0.001	0.15	0.01		
TP ₄	6.76	3.75	< 0.001	< 0.001	0.006	< 0.001	1	
TP ₅	5.06	4.04	0.002	0.002	0.65	0.02	1	0.01

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *p* values with Bonferroni correction for multiple comparisons. No *p*-value was calculated for the TP₋₁ and TP₀ comparison due to a lack of variability in the results; we imputed a *p*-value of 1.

Post-hoc tests showed statistically significant differences between all the time points, except for TP₋₁ and TP₀, TP₁ and TP₂, TP₁ and TP₃, TP₁ and TP₅, TP₃ and TP₄, and TP₃ and TP₅ (**Figure 10**).

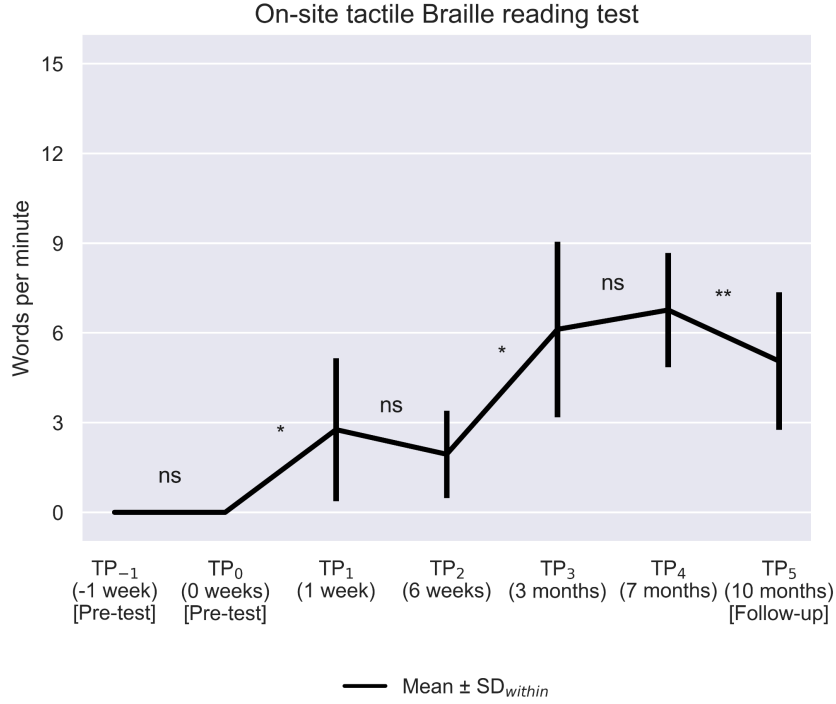


Figure 10. Tactile word reading speed during training. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

4.2.1.2. fMRI Lexical Decision Tasks

Visual Braille

To test the effect of training on the accuracy of answers in the visual Braille LDT, we computed a 7 (time: TP₁ - TP₅) $\times$ 2 (condition: experimental word/pseudoword blocks vs control symbol-detection blocks) repeated-measures ANOVA. We observe a statistically significant effect of time and condition interaction, $F(6, 96) = 17.88$; $p < 0.001$; $\eta^2_p = 0.533$. **Table 7** shows Bonferroni-corrected post-hoc comparisons between all the time points in the experimental condition:

Table 7. Bonferroni-corrected paired t-tests comparing time points within the experimental condition of the visual Braille LDT.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	49.99	5.51						
TP ₀	51.26	5.12	1					
TP ₁	54.24	6.97	1	1				
TP ₂	60.16	9.53	0.024	0.042	1			
TP ₃	59.19	14.06	1	1	1	1		
TP ₄	67.21	10.30	0.001	0.002	0.012	1	0.252	
TP ₅	64.29	9.60	0.02	0.007	0.361	1	1	1

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *p* values with Bonferroni correction for multiple comparisons.

Post-hoc tests showed statistically significant differences between TP₋₁ and TP₂, TP₋₁ and TP₄, TP₋₁ and TP₅, TP₀ and TP₄, TP₀ and TP₅, and TP₁ and TP₄ (**Figure 11**).

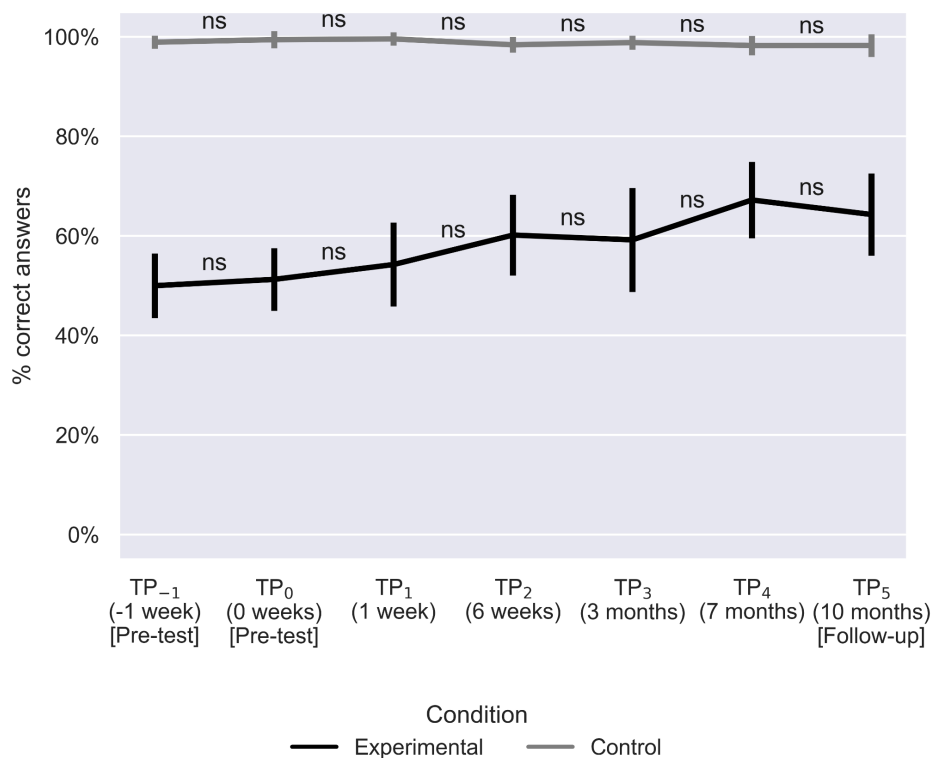


Figure 11. Correctness in experimental and control blocks of the Visual Braille Lexical Decision Task. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

Tactile Braille

To test the effect of training on the correctness of answers in the tactile Braille LDT, we computed a 7 (time: TP₋₁ - TP₅) $\times$ 2 (condition: experimental word/pseudoword blocks vs

control symbol-detection blocks) repeated-measures ANOVA. We observe a statistically significant effect of time and condition interaction, $F(6, 96) = 7.05$; $p = 0.001$; $\eta^2_p = 0.31$.

Table 8 shows Bonferroni-corrected post-hoc comparisons between all the time points in the experimental condition:

Table 8. Bonferroni-corrected paired t-tests comparing time points within the experimental condition of the tactile Braille LDT.

Time point	<i>M</i>	<i>SD</i>	TP ₋₁	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₋₁	51.42	8.47						
TP ₀	50.25	5.69	1					
TP ₁	58.77	7.92	0.309	0.013				
TP ₂	64.16	10.27	0.058	0.015	1			
TP ₃	69.18	15.46	0.111	0.011	0.424	1		
TP ₄	67.87	14.64	0.045	0.006	0.836	1	1	
TP ₅	68.79	13.74	0.083	0.004	0.424	1	1	1

Note. TP₋₁ = Pre-test (one week before the course), TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *p* values with Bonferroni correction for multiple comparisons.

Post-hoc tests showed statistically significant differences between TP₋₁ and TP₄, TP₀ and all the other time points (**Figure 12**).

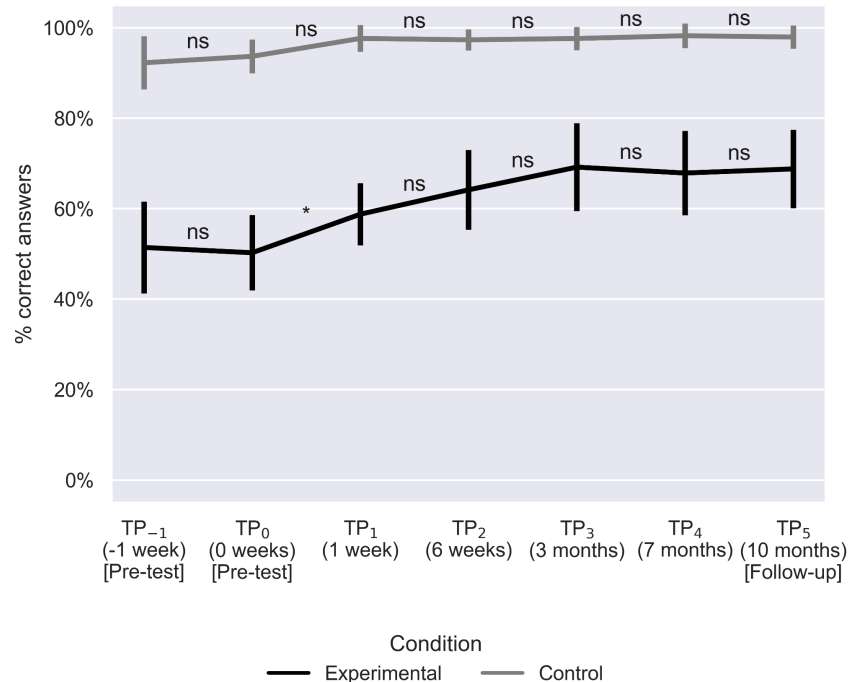


Figure 12. Correctness in experimental and control blocks of the tactile Braille Lexical Decision Task. Error bars represent standard deviations adjusted for within-subject designs (Cousineau, 2005). To improve clarity, only adjacent time point contrasts are displayed. *** - $p < 0.001$, ** - $p < 0.01$, * - $p \leq 0.05$, ns - $p > 0.05$. Bonferroni corrected.

4.2.2. fMRI Results

4.2.2.1. Print Lexical Decision Task

Main effect of condition

Collapsing across all sessions, the print Lexical Decision Task (experimental > control conditions) elicited significant increases in activity in both hemispheres, with large clusters in the left inferior frontal gyrus (opercular, triangular, and orbital parts), left precentral and postcentral gyri, as well as the left insula (see **Table 9** and **Figure 13**). A parallel cluster encompassed the right inferior frontal gyrus (opercular, triangular, orbital parts) and the right insula in the right hemisphere. The left inferior temporal gyrus (including the VWFA region) also exhibited stronger responses for word processing, along with portions of the left superior temporal gyrus. Outside the frontal-temporal network, bilateral occipital areas (calcarine cortex and cuneus) showed increased activation for word blocks, indicating a greater demand for visual processing. Furthermore, subcortical peaks emerged in the left hippocampus, caudate, and thalamus, and bilateral cerebellar regions (e.g., right lobule VI, bilateral Crus II, and part of the vermis) were also more active during the experimental condition than during the control condition. These patterns collectively underscore the engagement of language-related and supporting sensorimotor, subcortical, and cerebellar circuits during the processing of actual print words versus non-linguistic symbols.

Table 9. The main effect of condition in the print Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Opercular part of the inferior frontal gyrus	2818	23.27	-49	10	26
L Triangular part of the inferior frontal gyrus		18.26	-54	30	6
L Orbital part of the inferior frontal gyrus		18.02	-42	30	-4
L Postcentral gyrus		16.47	-56	-8	46
L Precentral gyrus		13.07	-44	-2	39
L Insula		6.17	-24	12	-21
R Opercular part of the inferior frontal gyrus	1465	14.36	44	10	26
R Insula		13.55	36	22	-4
R Triangular part of the inferior frontal gyrus		10.94	54	30	19
R Orbital part of the inferior frontal gyrus		10.92	48	40	-6
L Supplementary motor area	963	16.23	-2	22	52
L Medial part of the superior frontal gyrus		6.96	-6	42	36
L Calcarine cortex	897	10.05	-12	-75	12
R Calcarine cortex		9.81	24	-70	9
R Cuneus		7.81	4	-88	24
L Inferior temporal gyrus	521	21.01	-46	-42	-16
L Inferior occipital gyrus		7.39	-42	-75	-8
L Middle temporal gyrus	405	13.41	-52	-40	4
L Superior temporal gyrus		9.94	-56	-25	2
R Lobule VI of cerebellar hemisphere	335	9.40	11	-75	-21
L Crus II of cerebellar hemisphere		8.43	-6	-78	-28
R Crus II of cerebellar hemisphere		7.90	28	-78	-41
L Hippocampus	185	8.63	-29	-15	-11
L Caudate	113	7.71	-14	10	6
L Thalamus	77	7.61	-14	-15	12
R Lobule VIII of vermis	68	5.99	1	-60	-34
R Caudate	21	6.31	11	15	6

Note. Local peaks from a contrast represent a paired t-test comparison of experimental > control contrasts for all time points. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

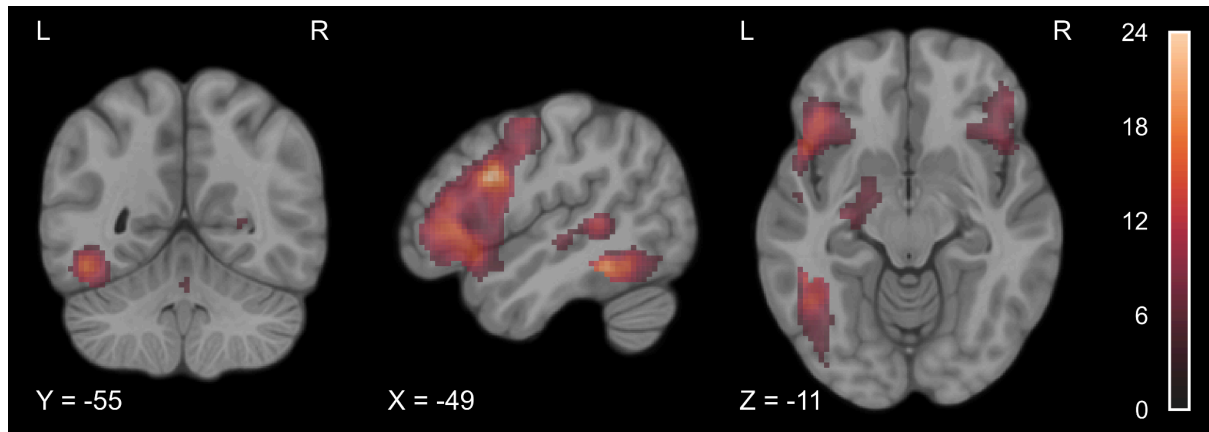


Figure 13. Statistical map of the main effect of condition (experimental > control contrast) in the print Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

The effect of task repetition

We computed a paired t -test comparison of the experimental > control contrasts for the two pre-training time points (TP₀ and TP₁) to control the repetition effect without learning. The analysis revealed no significant activity differences between the time points.

The main effect of time and pairwise comparisons

We calculated a one-way rmANOVA to control for the repetition effect of print LDT without a learning component. The analysis revealed no significant effect of time or activity differences between time points.

4.2.2.2. Tactile Braille Lexical Decision Task

Main effect of condition

When comparing Braille word blocks against non-linguistic control blocks across all time points, extensive bilateral activation was observed (see **Table 10** and **Figure 14**). The left hemisphere showed involvement of the opercular and triangular parts of the inferior frontal gyrus, the supplementary motor area, the precentral gyrus, the superior parietal lobule, and the inferior temporal gyrus, all reflecting a strong motor-linguistic network for processing Braille by touch. Subcortical regions like the thalamus were also more active.

On the right side, the precentral gyrus and superior frontal gyrus showed a similarly greater response to Braille words, implying bilateral executive-motor engagement. Additionally, inferior parietal and occipital areas in both hemispheres (e.g., superior/middle occipital gyri) were more active, suggesting visuospatial or attentional components were co-opted for tactile

letter decoding. Furthermore, the cerebellum (notably lobule VI) demonstrated heightened activation on the right, underscoring the role of coordinated finger movements and error correction in Braille reading.

Overall, these findings highlight a broad sensorimotor-linguistic circuit that underpins tactile Braille word recognition. This circuit spans bilateral frontal-parietal regions, subcortical relays (thalamus), and ventral occipitotemporal pathways in the left hemisphere. This extensive pattern underscores the intensive motor, sensory, and linguistic demands of reading Braille by touch.

Table 10. The main effect of condition in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Opercular part of the inferior frontal gyrus	25033	29.28	-49	10	29
L Supplementary motor area		28.82	-4	2	59
L Superior occipital gyrus		25.38	-26	-72	39
L Precentral gyrus		24.54	-54	0	46
L Inferior parietal lobule		24.28	-32	-50	44
R Lobule VI of cerebellar hemisphere		23.57	28	-70	-24
L Inferior temporal gyrus		23.20	-49	-58	-11
R Superior occipital gyrus		21.38	28	-70	42
R Inferior parietal lobule		21.36	44	-35	46
L Triangular part of the inferior frontal gyrus		20.66	-34	30	4
L Superior parietal lobule		20.38	-26	-68	54
R Superior frontal gyrus		20.01	24	-2	54
R Precentral gyrus		19.94	54	8	39
L Thalamus		19.79	-14	-15	9
L Middle temporal gyrus	104	8.81	-59	-38	6

Note. Local peaks from a contrast represent a paired t-test comparison of experimental > control contrasts for all time points. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

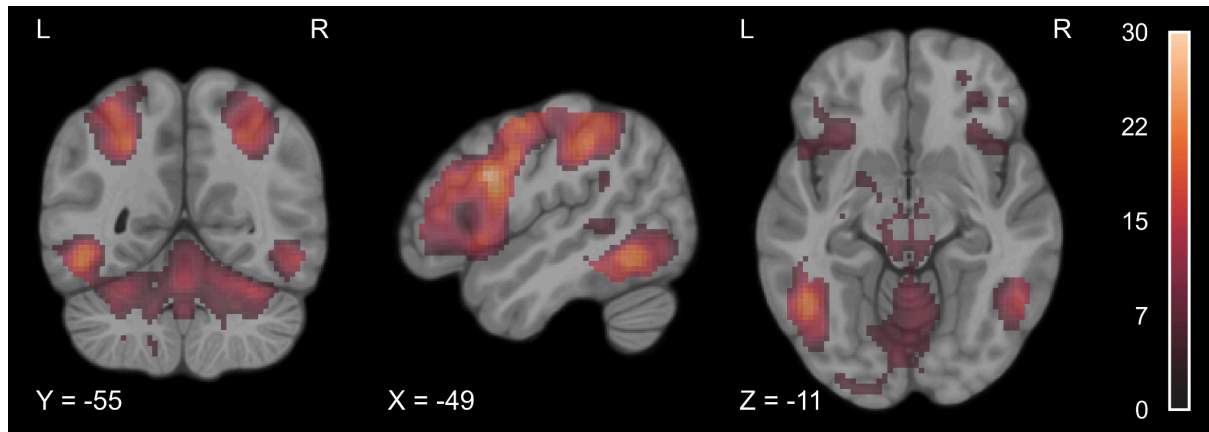


Figure 14. Statistical map of the main effect of condition (experimental > control contrast) in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

The effect of task repetition

Before learning Braille, participants completed the task twice (at TP_{-1} and TP_0 , one week apart). A direct comparison between these two pre-training sessions revealed no significant differences in brain activation. In other words, simply repeating the tactile Braille task once did not alter the functional response. This confirms that any longitudinal changes observed can be attributed to the introduction of Braille training rather than to task familiarisation.

Main effect of time

A rmANOVA on the tactile Braille Lexical Decision Task revealed significant changes in activation over time (see **Table 11** and **Figure 15**). In the left hemisphere, the largest cluster was centred on the inferior parietal lobule, extending into the superior parietal lobule, middle occipital gyrus, inferior frontal gyrus (both opercular and triangular parts), and portions of the middle and superior frontal gyri. Nearby areas such as the precentral gyrus, postcentral gyrus, and insula also exhibited a significant time effect. An analogous network of parietal-frontal regions in the right hemisphere showed time-related changes, including the right inferior parietal lobule, superior occipital gyrus, supramarginal gyrus, and precentral gyrus. Additionally, midline structures like the bilateral supplementary motor area, median cingulate gyrus, and precuneus were implicated, as were subcortical and cerebellar regions, for instance, bilateral thalamus, portions of the caudate and putamen on the left, and the cerebellar hemispheres (lobule VI) and vermis (lobules IV-V, VIII) on the right. Several temporal-lobe sites also showed significant F -values, including the inferior temporal gyrus,

middle temporal gyrus, and fusiform gyrus in both hemispheres, as well as the left hippocampus.

The significant main effect of time in this broad set of cortical, subcortical, and cerebellar regions underscores that Braille processing demands were not static throughout the training and follow-up period, indicating adaptive reorganisation in multiple functional networks over the study's duration.

Table 11. The main effect of time in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>F</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior parietal lobule	4101	47.26	-52	-28	42
L Opercular part of the inferior frontal gyrus		39.07	-52	8	29
L Superior parietal lobule		38.02	-39	-50	62
L Middle frontal gyrus		33.98	-26	-8	52
L Precentral gyrus		33.79	-56	0	44
L Middle occipital gyrus		28.79	-29	-72	32
L Insula		25.65	-34	20	4
L Superior frontal gyrus		14.10	-22	-2	74
L Postcentral gyrus		13.52	-62	-18	22
L Triangular part of the inferior frontal gyrus		11.87	-52	28	26
R Inferior parietal lobule	1666	50.56	44	-35	46
R Superior occipital gyrus		30.76	26	-65	46
R Supramarginal gyrus		18.57	58	-18	29
L Median cingulate gyrus	1423	54.14	-14	-42	36
R Precuneus		45.38	14	-50	39
L Precuneus		33.32	-2	-55	36
R Median cingulate gyrus		14.39	1	-22	44
L Angular gyrus	938	55.97	-42	-58	26
R Angular gyrus	851	42.58	54	-62	26
R Lobule VI of cerebellar hemisphere	841	30.80	28	-68	-24
R Lobule IV, V of vermis		16.75	1	-50	-21
R Lobule VIII of vermis		11.47	1	-70	-38
L Supplementary motor area	800	41.29	-4	2	56
R Supplementary motor area		30.00	4	15	49
R Precentral gyrus	606	31.01	54	8	36
L Middle frontal gyrus	477	22.48	-39	18	44
L Superior frontal gyrus		13.93	-19	35	39
R Superior frontal gyrus	381	44.24	24	-5	54
R Middle frontal gyrus		11.23	46	0	56
L Lobule VI of cerebellar hemisphere	319	26.54	-26	-70	-24
R Superior frontal gyrus	264	20.66	16	30	56
R Middle frontal gyrus		14.67	38	20	52
L Anterior cingulate gyrus	240	17.46	-12	50	-1

R Medial part of the superior frontal gyrus		12.62	4	60	12
R Inferior temporal gyrus	210	16.72	44	-5	-36
R Middle temporal gyrus		14.28	58	-2	-16
R Temporal pole (middle)		12.71	48	8	-28
R Fusiform gyrus	189	20.47	26	-35	-18
L Inferior temporal gyrus	162	20.25	-49	-55	-11
L Putamen	159	15.92	-19	10	6
L Thalamus	136	29.79	-14	-15	9
R Thalamus		21.46	11	-12	4
R Caudate		11.72	11	10	2
L Hippocampus	66	14.48	-26	-20	-18
L Fusiform gyrus		11.00	-29	-40	-14
L Middle temporal gyrus	56	16.20	-46	5	-31
R Rolandic operculum	55	27.98	41	-15	22
R Inferior temporal gyrus	49	18.49	54	-55	-11
L Middle temporal gyrus	22	15.21	-64	-18	-6
L Insula	20	13.19	-39	-20	22

Note. Local peaks from a contrast represent the effect of time ($TP_0 - TP_5$) for experimental > control contrast in a repeated measures ANOVA model. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

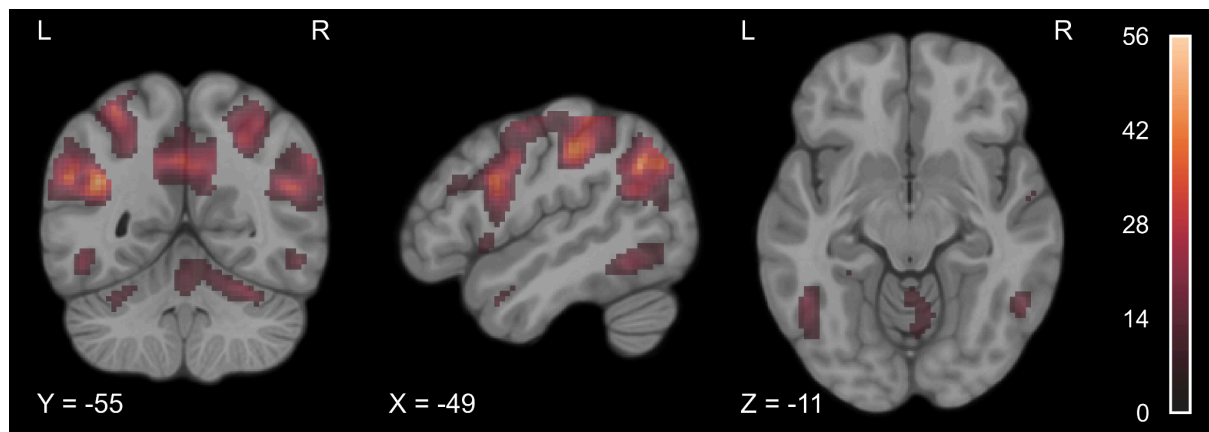


Figure 15. Statistical map of the main effect of time (experimental > control contrast) in the tactile Lexical Decision Task. The colour map represents the F -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

Pairwise comparisons

Following the F-test, we conducted a series of follow-up analyses using paired t-tests to check the pattern of activity change compared to the pre-scan at TP_0 .

$$TP_1 > TP_0$$

After 7 days of Braille instruction, comparing fMRI activation at TP_1 with the pre-training baseline (TP_0) revealed several bilateral networks that showed higher activation in the experimental than in the control condition (see **Table 12** and **Figure 16**). A large left inferior parietal lobule cluster encompassed peaks in the left superior parietal lobule, left middle occipital gyrus, and postcentral gyrus. Together, these suggest early enhancement of sensorimotor and spatial-attentional processes for tactile reading even within the first week. A similarly large cluster peaking in the right inferior parietal lobule in the right hemisphere included sub-peaks in the right superior occipital gyrus, angular gyrus, superior parietal lobule, and supramarginal gyrus.

Prefrontal cortex involvement appeared as well. A left inferior frontal gyrus opercular cluster showed significantly higher activation at TP_1 and the neighbouring left precentral gyrus and left superior frontal region. In parallel, a left supplementary motor area cluster also incorporated a sub-peak in the right supplementary motor area. Additional frontal changes included a right superior frontal gyrus cluster and a smaller right precentral gyrus cluster.

Of note, occipital activations were already present at TP_1 in the left middle occipital gyrus (part of the left inferior parietal lobule cluster) and the right superior occipital gyrus (within the right inferior parietal lobule cluster).

Subcortical and cerebellar regions also contributed. The left thalamus was significantly more active at TP_1 . The right thalamus also surpassed the threshold, though at a slightly lower t-value. The left putamen also exhibited increased activation. Bilateral cerebellar lobule VI clusters were present, potentially indicating improved sensorimotor coordination in the emergent Braille-reading finger movements.

In summary, one week of Braille practice produced a broad pattern of heightened engagement across bilateral parietal, frontal, subcortical, and cerebellar areas, with some occipital involvement (middle and superior occipital gyri) already appearing. These changes likely reflect the brain's initial adaptation to a novel tactile-linguistic skill, laying the groundwork for more specialised cross-modal or language-related reorganisation observed in subsequent months.

Table 12. The comparison of $TP_1 > TP_0$ in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior parietal lobule	1720	10.45	-52	-28	42
L Superior parietal lobule		8.88	-29	-65	52
L Middle occipital gyrus		7.72	-29	-70	32
L Postcentral gyrus		5.85	-62	-18	22
R Inferior parietal lobule	1394	10.89	44	-35	46
R Superior occipital gyrus		8.70	31	-70	44
R Angular gyrus		8.50	28	-55	46
R Superior parietal lobule		7.83	26	-60	62
R Supramarginal gyrus		7.01	58	-15	29
L Opercular part of the inferior frontal gyrus	1216	9.73	-52	10	29
L Precentral gyrus		9.02	-56	0	44
L Superior frontal gyrus		6.74	-22	2	64
L Supplementary motor area	778	10.07	-4	2	56
R Supplementary motor area		9.93	4	15	49
R Median cingulate gyrus		5.97	8	20	32
R Superior frontal gyrus	324	9.62	26	-5	54
L Insula	262	8.11	-34	20	4
R Precentral gyrus	178	8.20	54	5	39
R Opercular part of the inferior frontal gyrus		8.16	54	8	24
L Middle frontal gyrus	149	6.95	-44	45	16
L Triangular part of the inferior frontal gyrus		6.27	-52	28	29
R Lobule VI of cerebellar hemisphere	116	7.63	28	-70	-24
L Thalamus	88	7.66	-12	-15	6
L Lobule VI of cerebellar hemisphere	87	7.43	-26	-70	-26
R Thalamus	52	6.53	11	-12	4
L Putamen	22	5.44	-22	-2	4

Note. Local peaks from a contrast represent a paired t-test comparison of $TP_1 > TP_0$ for experimental > control contrasts. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

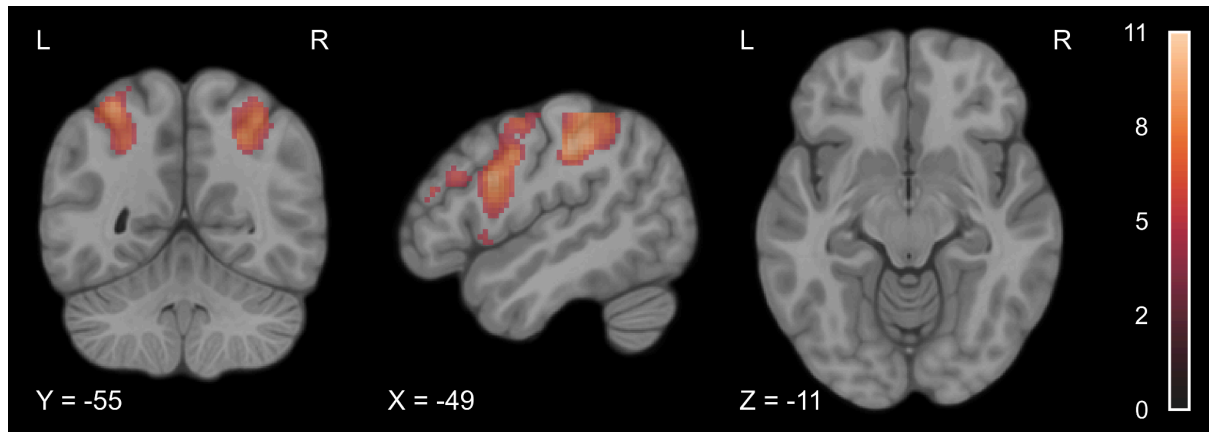


Figure 16. Statistical map of the paired t-test comparison of $TP_1 > TP_0$ for experimental > control contrast in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The coordinates on the map represent the peak of activity in the visual word form area in all Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p-value of 0.05 and a cluster extent of 20 voxels.

$TP_2 > TP_0$

Six weeks into Braille training, a comparison with the pre-training baseline showed widespread increases in activation for tactile word processing relative to control stimuli (see **Table 13** and **Figure 17**). In the left hemisphere, these changes encompassed the inferior and superior parietal lobules, the precentral and postcentral gyri, and the insula, as well as frontal areas including the opercular and triangular parts of the inferior frontal gyrus, the superior frontal gyrus, and the supplementary motor area. The left inferior temporal gyrus (including the VWFA) also emerged at this stage.

In the right hemisphere, the supramarginal gyrus and adjacent superior parietal and occipital regions were significantly more active at TP_2 compared to baseline, mirroring left-sided parietal-occipital changes. Frontal involvement extended to the right precentral gyrus, inferior frontal gyrus (opercular region), and superior frontal gyrus, indicating bilateral executive and motor recruitment for tactile reading.

Subcortical and cerebellar structures likewise showed heightened activation. At six weeks, both the left and right thalamus, along with the left putamen and the right caudate, were more active, suggesting deeper adaptation within sensorimotor and integrative pathways. The cerebellum also presented bilateral engagement across multiple lobules, consistent with refined motor coordination of Braille scanning movements.

Overall, the results indicate a broadened pattern of cortical and subcortical participation after six weeks of Braille practice. In addition to the parietal and frontal regions, the occipital cortex (including portions of the superior occipital gyrus) became notably involved,

suggesting that tactile reading may draw upon (or co-opt) specific visual-associative resources, even in sighted participants who rely on touch. The inferior temporal and frontal-subcortical changes further indicate growing complexity and efficiency in the representation of Braille word recognition compared to the baseline state.

Table 13. The comparison of $TP_2 > TP_0$ in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior parietal lobule	4442	13.18	-52	-28	42
L Superior parietal lobule		11.97	-29	-65	56
L Opercular part of the inferior frontal gyrus		11.16	-52	10	29
L Postcentral gyrus		11.09	-49	-35	56
L Superior frontal gyrus		10.85	-26	-8	59
L Precentral gyrus		10.16	-54	0	46
L Insula		9.37	-29	25	4
L Triangular part of the inferior frontal gyrus		6.17	-42	28	24
R Supramarginal gyrus	1915	13.33	41	-35	44
R Superior occipital gyrus		10.77	26	-65	46
R Superior parietal lobule		10.12	36	-52	56
R Lobule VI of cerebellar hemisphere	1626	10.69	28	-68	-24
L Lobule VI of cerebellar hemisphere		9.88	-26	-70	-24
L Lobule IV, V of vermis		8.14	-2	-50	-21
R Crus I of cerebellar hemisphere		7.80	8	-75	-24
L Lobule VIII of vermis		6.43	-2	-65	-31
R Lobule IV, V of cerebellar hemisphere		6.42	8	-60	-11
L Crus I of cerebellar hemisphere		5.43	-44	-62	-28
L Supplementary motor area	808	11.23	-6	5	54
R Median cingulate gyrus		5.64	11	20	36
R Precentral gyrus	601	9.41	54	8	36
R Opercular part of the inferior frontal gyrus		8.26	54	5	22
R Superior frontal gyrus	400	12.46	24	-5	54
R Middle frontal gyrus		5.96	48	2	54
L Inferior temporal gyrus	266	8.41	-49	-55	-11
L Putamen	210	7.26	-22	10	6
R Thalamus	170	8.20	14	-12	6
R Caudate		6.23	14	2	14
L Thalamus	163	9.16	-14	-15	9
R Inferior temporal gyrus	74	8.35	54	-55	-11
L Lobule VIII of cerebellar hemisphere	27	6.69	-16	-60	-48
L Rolandic operculum	22	7.42	-36	-5	14

Note. Local peaks from a contrast represent a paired t-test comparison of $TP_2 > TP_0$ for experimental > control contrasts. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

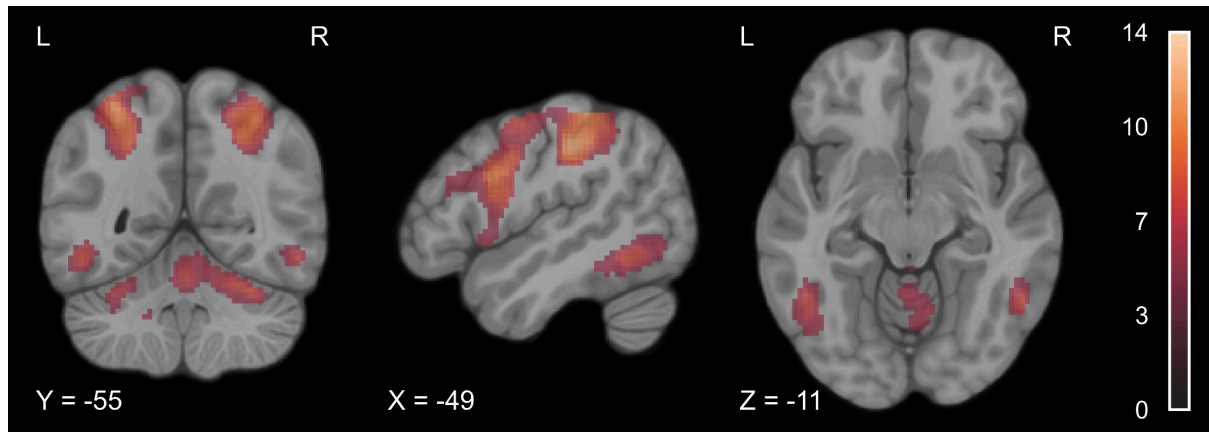


Figure 17. Statistical map of the paired t-test comparison of $TP_2 > TP_0$ for experimental > control contrast in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_3 > TP_0$

After approximately three months of Braille instruction, a direct comparison with the pre-training baseline revealed widespread activation increases for Braille word processing relative to control stimuli (see **Table 14** and **Figure 18**). In the left hemisphere, an extensive network spanned the inferior frontal gyrus (opercular and triangular parts), superior and middle frontal gyri, supplementary motor area, and pre- and postcentral gyri. The left inferior parietal lobule and superior parietal lobule also showed significant increases at this time point, reflecting heightened parietal involvement in tactile reading. Meanwhile, the left insula was more active, indicating continued engagement in attention- or salience-related processing. Notably, the left inferior temporal gyrus (consistent with the ventral occipitotemporal region, or VWFA) emerged as a key area of greater activation, suggesting that some portion of the visual word form circuit was recruited for Braille input.

In the right hemisphere, parietal regions, including the postcentral gyrus, superior occipital gyrus, and supramarginal gyrus, showed higher responses to Braille words than baseline, mirroring changes on the left. Bilateral frontal involvement was evident through the right superior frontal gyrus, middle frontal gyrus, and right precentral gyrus. Several subcortical and cerebellar structures likewise showed stronger activation at TP_3 , notably the left and right thalamus, the left and right caudate, and multiple lobules of the cerebellum (including lobule VI and vermis sections). These subcortical-cerebellar changes could underlie more profound sensorimotor adaptations necessary for skilled Braille scanning and integrating tactile information with higher-order processes.

After three months of practice, tactile Braille reading engaged extensive bilateral fronto-parietal areas, occipital cortex (especially on the right), and visual association regions in the left ventral temporal pathway (supportive of an orthographic-like representation for Braille). The thalamus, caudate, and cerebellum also showed significant deviations from baseline, further embedding the skill within motor and integrative circuits. This pattern underscores that, at TP₃, the network supporting Braille word recognition had become broader and more specialised than the pre-training state, potentially reflecting partial integration of tactile reading into the brain's reading/language circuitry.

Table 14. The comparison of TP₃ > TP₀ in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Opercular part of the inferior frontal gyrus	4753	11.78	-52	8	29
L Inferior parietal lobule		11.49	-52	-30	42
L Supplementary motor area		10.97	-4	2	56
L Precentral gyrus		10.22	-56	0	42
L Superior parietal lobule		10.18	-22	-65	42
L Middle frontal gyrus		10.00	-26	-8	52
L Insula		8.84	-34	20	4
L Postcentral gyrus		6.61	-64	-18	19
L Triangular part of the inferior frontal gyrus		6.49	-54	28	26
L Superior frontal gyrus	1598	5.72	-19	-8	76
R Median cingulate gyrus		5.54	8	20	32
R Postcentral gyrus		12.34	41	-32	46
R Superior occipital gyrus		9.70	26	-65	46
R Supramarginal gyrus		7.45	56	-18	29
R Precentral gyrus		10.15	54	8	36
R Superior frontal gyrus		11.44	26	-5	54
R Middle frontal gyrus		5.35	48	2	54
R Lobule VI of cerebellar hemisphere	193	8.90	28	-70	-24
L Lobule VI of cerebellar hemisphere		8.37	-26	-70	-24
R Crus I of cerebellar hemisphere		6.61	8	-75	-24
L Lobule IV, V of vermis		6.27	-2	-50	-21
R Lobule VIII of vermis		5.54	1	-60	-34
R Lobule IV, V of cerebellar hemisphere		5.39	8	-60	-11
L Inferior temporal gyrus		7.95	-49	-52	-11
L Caudate		6.19	-16	0	16
R Thalamus	145	8.27	11	-12	4
R Caudate		6.22	11	10	2
L Thalamus		10.02	-12	-15	6
R Inferior temporal gyrus	56	7.66	54	-55	-11

Note. Local peaks from a contrast represent the comparison of TP₃ > TP₀. The fMRI results represent a change in brain activation in the tactile LDT (experimental > control). Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

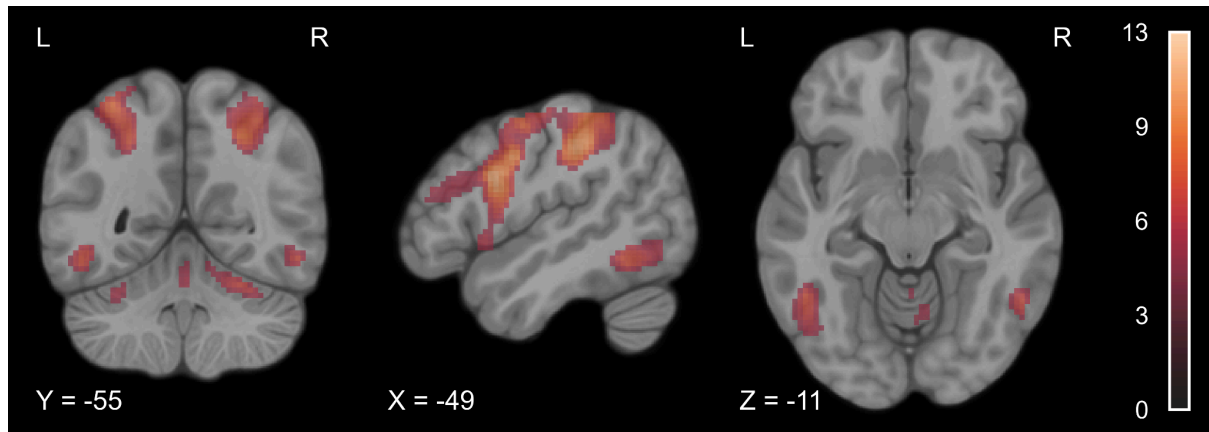


Figure 18. Statistical map of the paired t-test comparison of $TP_3 > TP_0$ for experimental > control contrast in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_4 > TP_0$

After seven months of Braille practice, a comparison with the baseline (TP_0) revealed broad increases in activation across both hemispheres (see **Table 15** and **Figure 19**). In the left hemisphere, the most extensive set of changes encompassed the inferior parietal lobule, supplementary motor area, superior parietal lobule, opercular and triangular parts of the inferior frontal gyrus, superior frontal gyrus, pre- and postcentral gyri, and the insula. Notably, the left middle occipital gyrus was again engaged, consistent with the participation of the dorsal visual stream in tactile reading. A separate peak in the left inferior temporal gyrus suggests that the VWFA was still engaged after 7 months of learning. The right inferior temporal gyrus was also more active, although to a lesser extent.

A parallel set of parietal and frontal regions in the right hemisphere displayed higher activity at TP_4 than at baseline. These included the right inferior parietal lobule, right superior parietal lobule, supplementary motor area, superior frontal gyrus, precentral gyrus, and middle frontal gyrus. Subcortical structures in both hemispheres, such as the left and right thalamus and putamen, showed significantly greater responses at seven months, likely reflecting deeper integration of tactile inputs into motor and relay circuits. The cerebellum likewise exhibited bilateral involvement across multiple lobules (including lobule VI and parts of the vermis), implicating ongoing motor coordination during Braille scanning.

Overall, after seven months of training, the contrast of TP_4 vs TP_0 revealed extensive engagement of left-lateralised language areas (inferior frontal, inferior temporal), bilateral parietal and frontal-motor networks, visual-association cortex (middle occipital, inferior

temporal), and subcortical-cerebellar domains. This pattern confirms the existence of a circuit for tactile word recognition that includes frontal-parietal control, somatosensory-motor integration, and the recruitment of typically “visual” regions for processing Braille shapes, all of which were more active than in the pre-training state.

Table 15. The comparison of $TP_4 > TP_0$ in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior parietal lobule	5309	12.33	-52	-28	42
L Supplementary motor area		12.02	-4	2	59
L Superior parietal lobule		11.11	-39	-50	62
L Opercular part of the inferior frontal gyrus		10.91	-52	10	29
L Superior frontal gyrus	10.58	10.58	-26	-8	59
L Precentral gyrus		10.56	-56	0	44
R Supplementary motor area		10.13	4	15	49
L Insula		9.45	-32	22	4
L Middle occipital gyrus	9.28	9.28	-29	-72	32
L Postcentral gyrus		7.46	-52	-20	56
R Median cingulate gyrus		6.55	8	22	32
L Triangular part of the inferior frontal gyrus		6.02	-42	28	24
R Inferior parietal lobule	1735	12.98	44	-35	46
R Superior parietal lobule		10.29	28	-52	49
R Supramarginal gyrus		7.84	56	-18	29
R Lobule VI of cerebellar hemisphere	1464	10.42	28	-68	-24
L Lobule VI of cerebellar hemisphere		9.68	-26	-70	-24
L Lobule IV, V of vermis		7.30	-2	-52	-24
R Lobule VIII of vermis		6.30	4	-70	-36
L Crus I of cerebellar hemisphere	5.56	5.56	-44	-62	-26
R Crus I of cerebellar hemisphere		5.54	46	-62	-28
R Superior frontal gyrus	1231	12.50	26	-5	54
R Precentral gyrus		10.58	54	8	36
R Middle frontal gyrus		6.90	46	0	56
R Thalamus	314	9.22	11	-12	4
R Putamen		6.97	21	8	6
L Putamen	228	7.58	-19	10	6
L Thalamus	196	10.41	-14	-15	9
L Inferior temporal gyrus	172	8.07	-49	-58	-8
R Inferior temporal gyrus	51	7.47	54	-58	-11
L Rolandic operculum	24	7.26	-36	-5	14

Note. Local peaks from a contrast represent the comparison of $TP_4 > TP_0$. The fMRI results represent a change in brain activation in the tactile LDT (experimental > control). All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

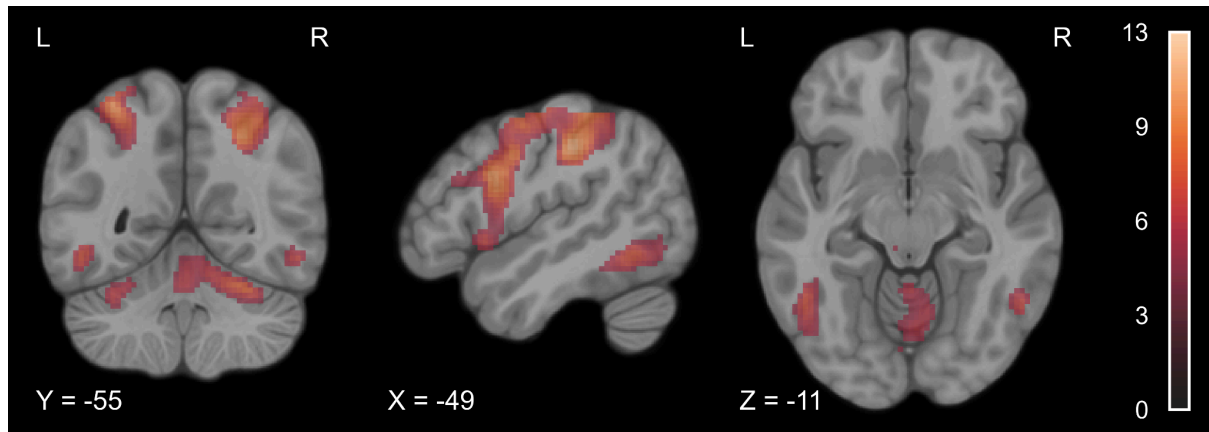


Figure 19. Statistical map of the paired t-test comparison of $TP_4 > TP_0$ for experimental > control contrast in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_5 > TP_0$

Three months after the conclusion of formal Braille training, the $TP_5 > TP_0$ comparison revealed that most of the brain areas previously associated with Braille word processing (vs control) retained significantly higher activation than at baseline (see **Table 16** and **Figure 20**). In the left hemisphere, stronger responses persisted in the inferior parietal lobule, superior parietal lobule, opercular part of the inferior frontal gyrus, pre- and postcentral gyri, supplementary motor area, and middle occipital gyrus, along with smaller peaks in the superior frontal gyrus and insular cortex. Notably, the left inferior temporal gyrus was again implicated in tactile reading, overlapping the VWFA.

In the right hemisphere, regions in the postcentral gyrus, superior parietal lobule, superior occipital gyrus, and supplementary motor area remained above baseline. The right insula also showed a moderate activation cluster at follow-up, indicating that some aspects of attentional or salience processing were preserved. Subcortically, both the left and right thalamus were still active above baseline, suggesting continued adaptation in sensory-relay pathways for Braille. Other basal ganglia structures (e.g., putamen, caudate) did not appear in the table at TP_5 , implying that any early training-related changes in these nuclei may have returned closer to baseline in the absence of ongoing practice.

At three months post-training, the core reading-related network (including parietal, frontal, and inferior temporal areas) remained engaged for Braille. At the same time, the occipital cortex on both sides continued to show higher activation than pre-training, consistent with the idea that cross-modal use of visual areas had become at least partially stabilised. These

findings suggest lasting neuroplastic changes that endure beyond active training, even if some ancillary regions (e.g., certain basal ganglia foci) no longer surpass the threshold once daily Braille reading ceases.

Table 16. The comparison of $TP_5 > TP_0$ in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior parietal lobule	3267	10.91	-52	-28	42
L Superior parietal lobule		10.46	-39	-50	62
L Opercular part of the inferior frontal gyrus		10.28	-52	8	29
L Precentral gyrus		10.27	-56	0	44
L Middle frontal gyrus		10.05	-26	-8	52
L Middle occipital gyrus		8.86	-29	-70	32
L Postcentral gyrus		7.25	-52	-20	56
L Superior frontal gyrus	1336	5.63	-22	-2	74
R Postcentral gyrus		11.05	41	-32	46
R Superior parietal lobule		8.31	28	-52	49
R Superior occipital gyrus		7.50	28	-70	39
R Supramarginal gyrus		5.97	56	-18	29
L Supplementary motor area	420	11.13	-6	2	56
R Supplementary motor area		7.03	6	15	49
R Superior frontal gyrus	257	10.10	26	-5	54
R Lobule VI of cerebellar hemisphere	245	8.38	26	-68	-24
R Precentral gyrus	195	8.66	54	8	36
L Insula	154	7.11	-32	22	4
L Lobule VI of cerebellar hemisphere	99	7.11	-26	-70	-24
R Insula	97	6.58	34	20	9
L Thalamus	94	8.76	-12	-15	6
L Inferior temporal gyrus	79	7.38	-49	-55	-14
R Thalamus	35	6.55	11	-12	4

Note. Local peaks from a contrast represent the comparison of $TP_5 > TP_0$. The fMRI results represent a change in brain activation in the tactile LDT (experimental > control). All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

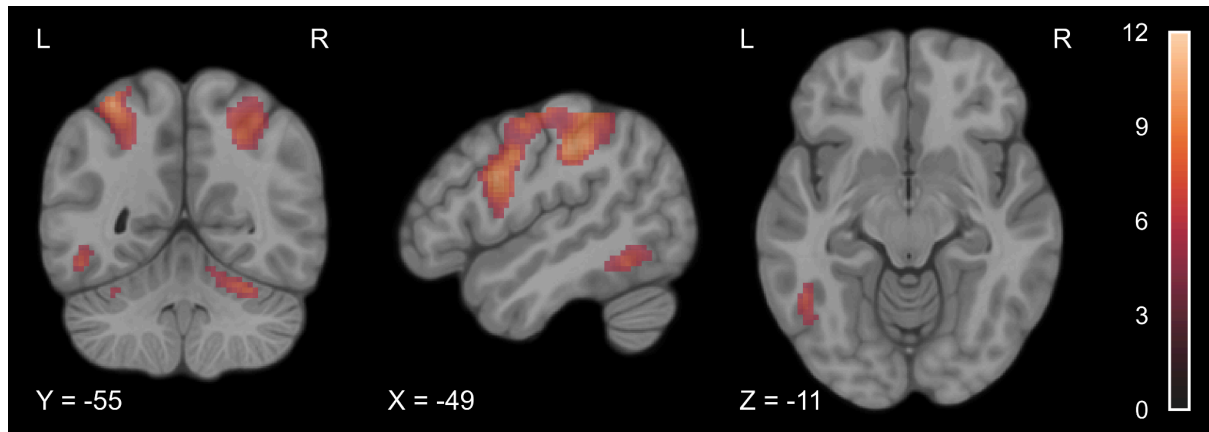


Figure 20. Statistical map of the paired t-test comparison of $TP_5 > TP_0$ for experimental > control contrast in the tactile Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

The comparison of all time points during learning

We performed a series of paired t-test comparisons of the experimental > control contrast across multiple time points during Braille learning ($TP_2 > TP_1$; $TP_3 > TP_1$; $TP_4 > TP_1$; $TP_5 > TP_1$; $TP_3 > TP_2$; $TP_4 > TP_2$; $TP_5 > TP_2$; $TP_4 > TP_3$; $TP_5 > TP_3$; $TP_5 > TP_4$). None of these comparisons revealed a significant difference in activity, indicating that the overall activation pattern for Braille words (relative to control) did not change substantially between these time points.

4.2.2.3. Visual Braille Lexical Decision Task

Main effect of condition

During the visual Braille LDT, a widespread network of cortical areas showed significantly higher activation in the experimental condition than in the control condition (see **Table 17** and **Figure 21**). A large cluster spanned left-hemisphere motor and language regions, including the supplementary motor area, opercular and triangular parts of the inferior frontal gyrus, the precentral gyrus, and the insula. The right hemisphere also contributed strongly: the right supplementary motor area, right-lateralised precentral and frontal opercular areas, and additional frontal subpeaks were active, mirroring the left-sided engagement.

Bilateral parietal involvement was present in the inferior and superior parietal lobules, consistent with the visual-spatial analysis of Braille dot patterns. The supramarginal gyrus in both hemispheres was recruited, potentially supporting working memory and/or phonological aspects of decoding. At the same time, the occipital cortex showed strong bilateral responses in the middle occipital gyrus, reflecting the processing of visually presented dot

configurations. Additionally, right-lateralised cerebellar lobules were involved, implying motor or attentional support for the visual Braille task.

Notably, the left inferior temporal gyrus emerged in this contrast, close to the typical coordinates of the VWFA. However, as participants did not train extensively in reading Braille by sight, the processing seemed more distributed across dorsal visual-stream (occipital-parietal) regions and bilateral frontal networks, indicating that participants approached visual Braille through a mixture of shape-based analysis and phonological decoding rather than fluent orthographic recognition.

In sum, while participants primarily learned Braille by touch, they nonetheless engaged substantial portions of the reading and visual attention networks when Braille letters were presented visually. This pattern suggests a partial cross-modal transfer of Braille knowledge, whereby the brain treats the unfamiliar dot shapes as potential orthographic stimuli, recruiting both visual shape-processing areas and language-related frontal/parietal regions.

Table 17. The main effect of condition in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Supplementary motor area	26724	32.51	-6	5	59
L Opercular part of the inferior frontal gyrus		32.22	-49	8	24
R Supplementary motor area		28.87	4	15	49
L Insula		27.01	-29	28	4
L Precentral gyrus		26.88	-49	-2	52
L Superior parietal lobule		26.10	-22	-65	42
R Lobule VI of cerebellar hemisphere		24.88	28	-68	-24
L Middle occipital gyrus		24.60	-29	-70	29
L Inferior parietal lobule		23.70	-39	-45	46
R Superior parietal lobule		22.99	26	-55	49
R Opercular part of the inferior frontal gyrus		22.65	51	10	29
R Middle occipital gyrus		22.23	31	-72	29
L Triangular part of the inferior frontal gyrus		22.22	-49	25	26
L Inferior temporal gyrus		20.98	-46	-60	-8
R Median cingulate gyrus		19.51	11	22	34
R Superior frontal gyrus		19.39	24	0	54
R Supramarginal gyrus		19.21	44	-38	44
L Supramarginal gyrus	65	8.35	-64	-42	24
L Middle temporal gyrus	54	7.70	-56	-45	9
R Orbital part of the middle frontal gyrus	38	8.21	26	50	-14
R Orbital part of the superior frontal gyrus		6.54	26	65	-6
L Lobule IX of cerebellar hemisphere	33	6.72	-4	-45	-46
L Lobule VIII of cerebellar hemisphere	21	9.11	-14	-62	-48

Note. Local peaks from a contrast represent a paired t-test comparison of experimental > control contrasts for all time points. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

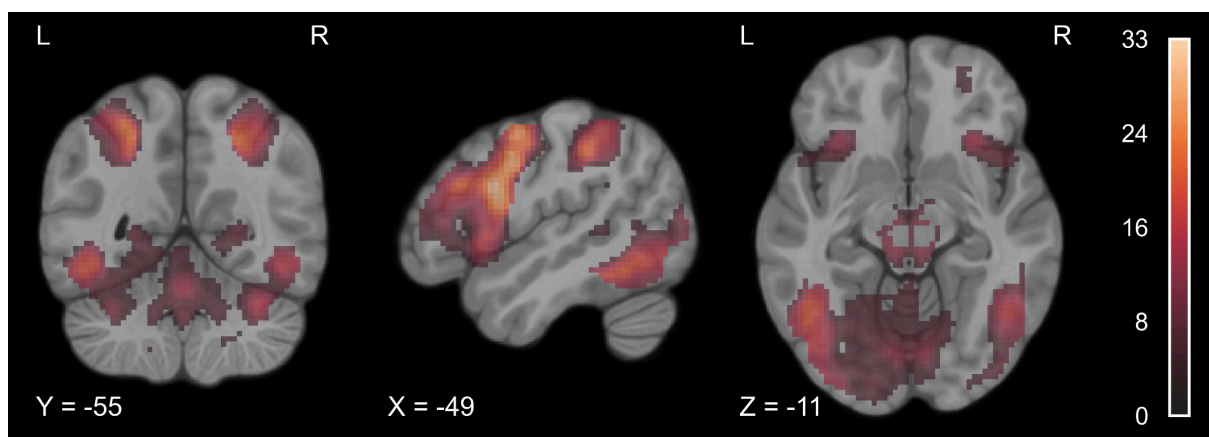


Figure 21. Statistical map of the main effect of condition (experimental > control contrast) in the visual Lexical Decision Task. The colour map represents the *t*-statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a *p*-value of 0.05 and a cluster extent of 20 voxels.

The effect of task repetition

As with the other tasks, we checked for differences between the two pre-training runs (TP₋₁ vs TP₀) for the visual Braille task. No significant differences were found, indicating that simply repeating the task once did not significantly change brain activation. Thus, any changes in activation over time for visual Braille can be attributed to cross-modal transfer from tactile learning, rather than mere repetition.

Main effect of time

A repeated-measures ANOVA on the visual Braille LDT identified significant changes across sessions in a range of cortical and subcortical regions (see **Table 18** and **Figure 22**). The inferior frontal gyrus (opercular and triangular parts), precentral gyrus, supplementary motor area, and insular cortex displayed alterations over time in the left hemisphere. The superior and inferior parietal lobules likewise showed a time effect, as did the inferior temporal gyrus and more posterior occipital sites (e.g., left inferior occipital gyrus). These findings indicate that the left-lateralised network for visual Braille shifted activity across the training period.

On the right side, changes were observed in parietal-frontal regions such as the superior parietal lobule, precentral gyrus, middle frontal gyrus, supplementary motor area, and insula. Occipital areas, including the right superior occipital gyrus, also demonstrated a significant effect of time, potentially reflecting the evolving visual processing of dot patterns. Subcortical and cerebellar structures also contributed, with the thalamus and multiple cerebellar lobules (e.g., left lobule VI, left vermis) meeting the threshold for time-related changes.

Overall, these results show that visual Braille reading was not static. Despite the participants' primary training being tactile, their responses to Braille letters viewed visually changed significantly over the course of the study. This pattern suggests that the brain's reading and visual-attention networks adapted to the script in multiple cortical and subcortical regions over time, presumably reflecting participants' growing familiarity with Braille forms even in the visual modality.

Table 18. The main effect of time in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>F</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Precentral gyrus	1423	40.95	-46	-2	36
L Opercular part of the inferior frontal gyrus		30.62	-49	8	24
L Insula		25.80	-32	28	4
L Triangular part of the inferior frontal gyrus		14.51	-39	28	22
L Superior parietal lobule	1256	29.67	-26	-62	56
L Middle occipital gyrus		24.12	-29	-75	24
L Inferior parietal lobule		20.78	-39	-45	46
R Calcarine cortex	631	18.29	11	-75	14
L Calcarine cortex		16.76	-6	-82	6
L Supplementary motor area	618	41.30	-4	2	62
R Supplementary motor area		21.72	6	12	49
R Median cingulate gyrus		15.92	11	20	34
L Median cingulate gyrus	554	20.25	-4	-48	34
L Precuneus		11.71	-4	-68	36
L Angular gyrus	543	39.65	-42	-72	46
R Lobule VI of cerebellar hemisphere	499	26.95	28	-68	-24
L Lobule VI of cerebellar hemisphere		16.80	-9	-75	-16
R Angular gyrus	443	23.72	44	-68	36
R Inferior parietal lobule		14.88	54	-58	44
R Superior parietal lobule	308	21.02	24	-65	56
R Superior occipital gyrus		17.54	28	-78	32
R Superior frontal gyrus	300	16.96	26	0	56
R Middle frontal gyrus		13.77	46	0	52
R Precentral gyrus		13.59	48	5	34
L Inferior temporal gyrus	254	17.45	-46	-60	-8
L Inferior occipital gyrus		12.28	-42	-75	-8
R Superior frontal gyrus	136	16.95	24	30	52
R Middle frontal gyrus		10.45	36	20	49
L Superior frontal gyrus	115	14.94	-19	30	59
L Lobule IV, V of vermis	105	14.55	-2	-50	-21
L Lobule VI of cerebellar hemisphere	93	13.00	-32	-70	-21
R Supramarginal gyrus	76	12.53	44	-35	44
R Insula	66	14.96	36	-15	19
L Thalamus	49	15.94	-12	-15	6
L Medial part of the superior frontal gyrus	43	12.11	-9	62	19
R Medial orbital part of the superior frontal gyrus	39	11.73	1	60	-4
L Middle frontal gyrus	37	14.35	-39	15	46
L Rolandic operculum	22	13.44	-46	-20	19

Note. Local peaks from a contrast represent the effect of time ($TP_0 - TP_5$) for experimental > control contrast in a repeated measures ANOVA model. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

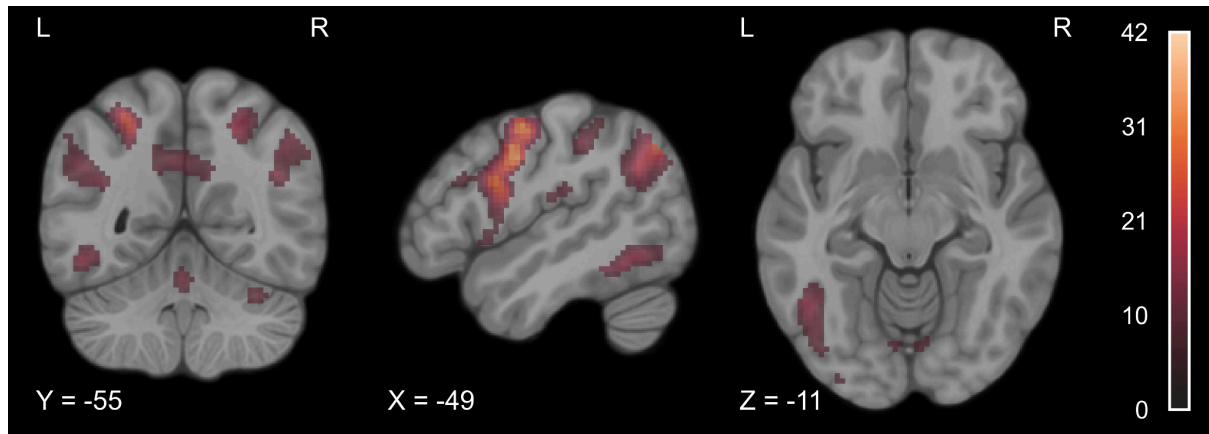


Figure 22. Statistical map of the main effect of time (experimental > control contrast) in the visual Lexical Decision Task. The colour map represents the F -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

Pairwise comparisons

We conducted a series of follow-up analyses using paired t -tests to check the pattern of activity change compared to pre-scan at TP_0 .

$$TP_1 > TP_0$$

After one week of tactile Braille learning, participants showed significant changes in activation when reading Braille visually (see **Table 19** and **Figure 23**). In the left hemisphere, notable increases spanned the supplementary motor area, precentral gyrus, insular cortex, and the opercular part of the inferior frontal gyrus, suggesting a combination of early phonological/articulatory processing and increased attentional demands. Additional peaks in the middle frontal gyrus and in the superior/inferior parietal and occipital regions (e.g., the middle occipital gyrus) indicate engagement of visual shape-processing and visuospatial networks.

On the right side, higher activation appeared in the supplementary motor area, median cingulate gyrus (dorsal anterior cingulate cortex), superior frontal gyrus, and precentral gyrus, and a smaller cluster in the opercular inferior frontal gyrus, indicating bilateral motor-linguistic involvement. The right insula also emerged, underscoring the novelty or salience attributed to visual Braille after only a short period of tactile training. Furthermore, parietal-occipital sites in the right hemisphere mirrored the left-side shape and attention processes. At the same time, bilateral cerebellar lobules (VI) were also engaged, consistent with the coordination aspects of reading a newly learned script.

Overall, these $TP_1 > TP_0$ results suggest that within just a week, the brain responds to visual Braille in a manner that reflects both linguistic-motor and visual-attentional demands. This pattern may represent an early cross-modal transfer, whereby recognising Braille as a meaningful script (initially learned by touch) influences how the brain processes it visually.

Table 19. The comparison of $TP_1 > TP_0$ in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Supplementary motor area	2484	10.90	-6	5	59
L Precentral gyrus		10.43	-46	-2	36
L Insula		9.75	-32	25	6
L Opercular part of the inferior frontal gyrus		9.61	-49	8	24
R Supplementary motor area		8.99	4	15	49
L Middle frontal gyrus		8.66	-26	-2	49
R Median cingulate gyrus		7.92	11	20	34
R Superior frontal gyrus		7.65	26	0	56
L Triangular part of the inferior frontal gyrus		7.20	-39	28	22
R Precentral gyrus		6.62	48	5	34
R Opercular part of the inferior frontal gyrus		5.40	46	8	16
L Superior parietal lobule	1001	8.48	-29	-62	54
L Inferior parietal lobule		8.14	-39	-45	46
L Middle occipital gyrus		7.56	-29	-75	24
L Superior occipital gyrus		7.01	-26	-75	39
R Superior parietal lobule	434	7.54	21	-65	56
R Supramarginal gyrus		6.74	44	-38	44
R Middle occipital gyrus		5.99	31	-75	29
R Insula	369	8.84	34	28	2
R Lobule VI of cerebellar hemisphere	125	7.23	28	-68	-24
L Inferior temporal gyrus	97	6.44	-46	-62	-8
R Middle frontal gyrus	63	6.80	36	48	26
L Middle frontal gyrus	42	6.50	-34	48	22
L Lobule VI of cerebellar hemisphere	36	5.46	-32	-62	-28
R Lobule VII of vermis	33	6.02	6	-75	-26

Note. Local peaks from a contrast represent a paired t-test comparison of $TP_1 > TP_0$ for experimental > control contrasts. All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

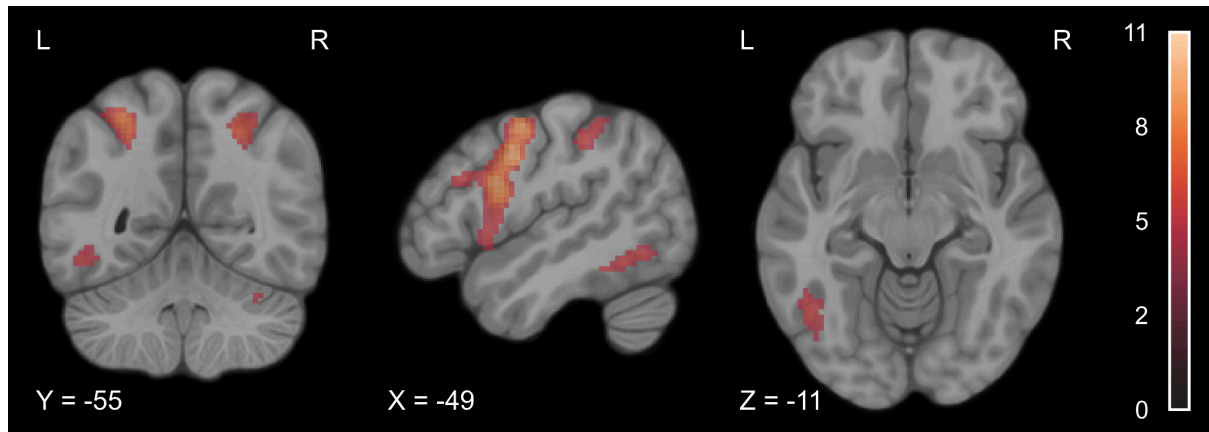


Figure 23. Statistical map of the paired t-test comparison of $TP_1 > TP_0$ for experimental > control contrast in the visual Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_2 > TP_0$

After about six weeks of primarily tactile Braille learning, participants showed significant activation increases during visual Braille LDT in both hemispheres (see **Table 20** and **Figure 24**). In the left hemisphere, changes encompassed the superior and inferior parietal lobules, as well as multiple occipital regions (including the inferior and middle occipital gyri and calcarine cortex), suggesting an expansion in visual-spatial processing for perceiving Braille dot patterns. Frontal-motor involvement on the left included the precentral gyrus, supplementary motor area, and the opercular and triangular parts of the inferior frontal gyrus, likely reflecting early phonological or articulatory coding for the novel script, along with attentional or executive demands.

The right hemisphere also exhibited significant parietal-occipital activity: the superior parietal lobule, superior occipital gyrus, and adjacent structures showed higher responses to visual Braille, indicating that dorsal stream shape analysis was bilaterally engaged. Additional right-lateralised clusters in the precentral gyrus, opercular inferior frontal gyrus, and supplementary motor area further point to a bilateral fronto-parietal effort in processing visual Braille. The left and right insulae appeared more active than at baseline, consistent with the sustained salience or attentional load associated with dealing with partially unfamiliar visual forms.

Subcortically, bilateral cerebellar lobules (including lobule VI) and portions of the vermis were implicated, suggesting that visual Braille reading, like tactile Braille, taps into motor-coordination networks. Meanwhile, the left inferior temporal gyrus (near the ventral

occipitotemporal region) showed greater activation, indicative of early orthographic or shape-based recognition processes specific to Braille. Overall, these $TP_2 > TP_0$ results underscore that after six weeks of tactile training, the visual system had begun adapting to Braille's dot patterns, recruiting visual-spatial, motor-linguistic, and cerebellar circuits to a greater extent than at baseline.

Table 20. The comparison of $TP_2 > TP_0$ in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Superior parietal lobule	1294	10.15	-26	-65	59
L Superior occipital gyrus		8.92	-26	-75	39
L Inferior parietal lobule		8.41	-39	-45	44
L Inferior occipital gyrus		6.04	-36	-90	-8
L Middle occipital gyrus		6.02	-42	-85	16
L Precentral gyrus	799	10.13	-46	-2	36
L Opercular part of the inferior frontal gyrus		8.84	-49	8	24
R Superior parietal lobule	786	8.29	24	-62	54
R Superior occipital gyrus		7.90	26	-72	39
R Supramarginal gyrus		6.21	44	-35	44
R Inferior parietal lobule		6.19	34	-48	42
R Lobule VI of cerebellar hemisphere	666	8.85	28	-68	-24
L Lobule VI of cerebellar hemisphere		7.31	-9	-75	-16
L Lobule VIII of vermis		6.76	-2	-60	-34
L Lobule IV, V of vermis		6.68	-2	-48	-21
L Supplementary motor area	451	9.80	-6	2	59
R Supplementary motor area		7.19	4	15	49
L Calcarine cortex	297	6.18	-6	-82	6
R Calcarine cortex		6.15	11	-75	14
R Cuneus		5.77	1	-88	19
L Inferior temporal gyrus	247	7.59	-46	-60	-8
L Inferior occipital gyrus		6.33	-42	-75	-8
R Superior frontal gyrus	232	7.09	24	0	56
R Precentral gyrus		6.13	44	0	49
R Opercular part of the inferior frontal gyrus		5.92	48	10	29
L Insula	220	7.91	-29	28	4
L Triangular part of the inferior frontal gyrus	23	6.00	-39	30	19
L Crus I of cerebellar hemisphere	22	5.96	-32	-62	-31

Note. Local peaks from a contrast represent a paired t-test comparison of $TP_2 > TP_0$ for experimental > control contrasts. Results were thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

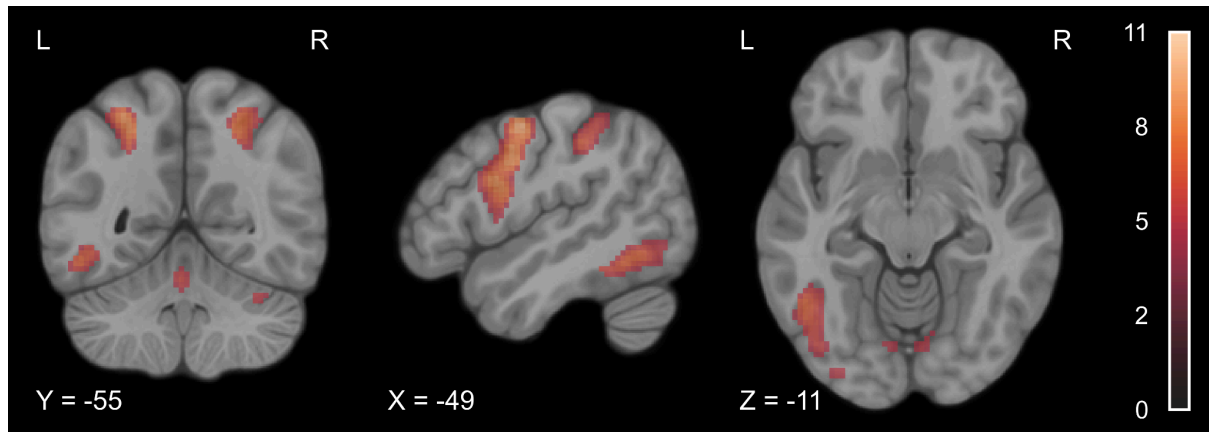


Figure 24. Statistical map of the paired t-test comparison of $TP_2 > TP_0$ for experimental > control contrast in the visual Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_3 > TP_0$

By three months of primarily tactile Braille instruction, a direct contrast of TP_3 vs baseline for the visual Braille task (experimental vs control) revealed widespread activation increases (see **Table 21** and **Figure 25**). In the left hemisphere, significant clusters included the precentral gyrus, the opercular and triangular parts of the inferior frontal gyrus, the supplementary motor area, and the insula, highlighting motor-linguistic engagement similar to that of tactile reading. The *visual word form area* was also recruited for Braille letter processing. Additionally, parietal and occipital changes (e.g., superior parietal lobule, inferior parietal lobule, middle/inferior occipital gyri, calcarine cortex) point to enhanced visual-spatial decoding of Braille dot patterns and potentially some orthographic-semantic mapping.

The right hemisphere showed analogous effects in frontal motor areas (right supplementary motor area, precentral gyrus, superior frontal gyrus) and visual regions (calcarine cortex, superior/middle occipital gyri, inferior parietal lobule). Subcortical and cerebellar sites were also involved in both hemispheres, notably the left and right thalamus, the left caudate, bilateral cerebellar lobule VI, and the vermis. These findings are consistent with cross-modal plasticity: although participants were not explicitly trained in *visual* Braille, their developing knowledge of Braille (acquired via touch) had begun to influence how the brain processed Braille letters by sight. By the three-month mark, visual Braille engaged a broad network that overlapped with tactile Braille, indicating a partial convergence of reading circuits across modalities.

Table 21. The comparison of $TP_3 > TP_0$ in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Precentral gyrus	1700	11.83	-46	-2	36
L Opercular part of the inferior frontal gyrus		9.97	-49	8	24
L Insula		9.40	-32	28	4
L Triangular part of the inferior frontal gyrus		7.33	-39	28	22
L Superior frontal gyrus		6.60	-22	5	62
L Supplementary motor area	667	11.11	-4	2	62
R Supplementary motor area		8.66	6	12	49
R Median cingulate gyrus		6.86	11	20	34
R Calcarine cortex	491	7.05	11	-75	14
L Calcarine cortex		6.97	-4	-78	9
R Superior frontal gyrus	401	7.47	24	0	54
R Precentral gyrus		7.20	48	5	34
R Lobule VI of cerebellar hemisphere	380	8.58	28	-68	-24
L Lobule VI of cerebellar hemisphere		6.43	-9	-75	-16
R Superior parietal lobule	375	8.19	24	-65	56
R Middle occipital gyrus		6.80	31	-78	32
R Superior occipital gyrus		5.63	26	-65	39
R Inferior parietal lobule		5.42	36	-50	54
L Inferior temporal gyrus	355	7.72	-49	-55	-11
L Lobule VI of cerebellar hemisphere		6.04	-32	-65	-26
L Superior parietal lobule	319	8.77	-26	-62	56
L Middle occipital gyrus		8.61	-29	-75	24
L Inferior parietal lobule		7.95	-39	-45	46
L Inferior occipital gyrus		6.44	-34	-90	-8
L Lobule IV, V of vermis	131	6.86	-2	-52	-18
R Inferior parietal lobule	125	6.32	44	-35	46
L Thalamus	123	7.38	-12	-15	6
R Thalamus	45	6.55	11	-15	14
L Caudate	36	6.52	-16	0	16
R Anterior cingulate gyrus	25	6.24	6	5	29
R Inferior temporal gyrus	23	5.66	51	-60	-11

Note. Local peaks from a contrast represent the comparison of $TP_3 > TP_0$. The fMRI results represent a change in brain activation in the visual LDT (experimental > control). All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

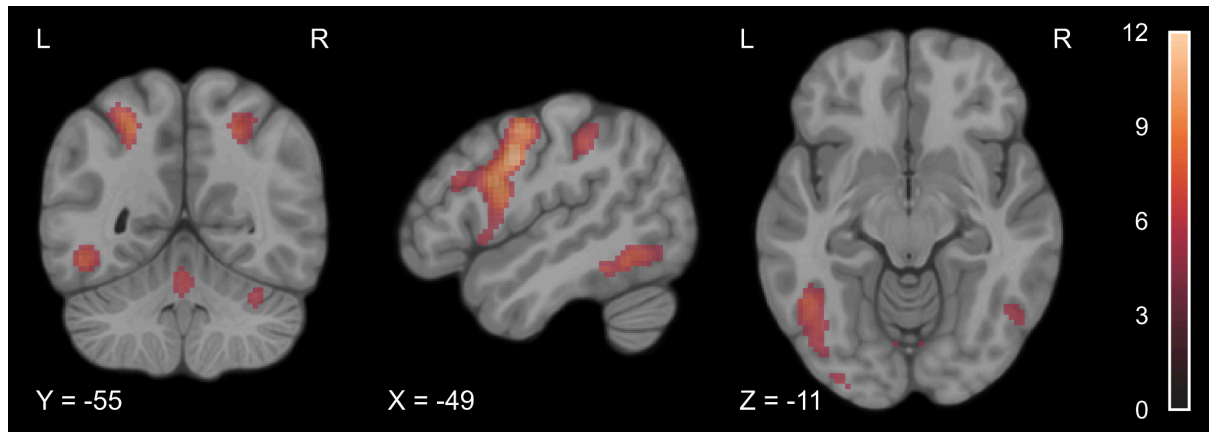


Figure 25. Statistical map of the paired t-test comparison of $TP_3 > TP_0$ for experimental > control contrast in the visual Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_4 > TP_0$

By the end of the Braille course (7 months), participants could identify Braille letters visually, albeit slowly, as reflected in the $TP_4 > TP_0$ contrast for visual Braille LDT (See **Table 22** and **Figure 26**). In the left hemisphere, significant activation increases were found in multiple parietal and occipital areas (e.g., superior parietal lobule, middle/inferior occipital gyri, calcarine cortex), as well as in inferior temporal regions, including the VWFA. Additionally, frontal-motor circuits (including the left precentral gyrus, supplementary motor area, and the opercular/triangular parts of the inferior frontal gyrus) indicated a phonological or articulatory component when viewing Braille letters. The left insula also appeared more active, suggesting continued salience or effort associated with decoding an unusual visual script.

In the right hemisphere, a broadly similar network emerged in the frontal-motor (right precentral gyrus, supplementary motor area), parietal-occipital (superior parietal lobule, middle/superior occipital gyri, cuneus), and insular areas, reflecting bilateral engagement for shape- and attention-related processing. Subcortical and cerebellar structures on both sides, such as the left and right thalamus, left putamen, and bilateral lobule VI of the cerebellum, were also above baseline, implying that reading Braille by sight, like tactile reading, tapped into sensorimotor and integrative pathways.

Overall, these results show that by TP_4 , visual Braille elicited a network that overlapped considerably with known language/reading areas (particularly the left ventral occipitotemporal cortex for orthographic processing) but still maintained bilateral support in

parietal-occipital and motor-attention regions. This suggests participants had successfully integrated some aspects of Braille letter recognition into the brain's visual reading machinery, leveraging both linguistic (e.g., the left inferior frontal gyrus) and spatial (parietal-occipital) processes to interpret Braille patterns visually.

Table 22. The comparison of $TP_4 > TP_0$ in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Superior parietal lobule	4387	10.41	-26	-62	56
R Lobule VI of cerebellar hemisphere		10.25	28	-68	-24
L Middle occipital gyrus		9.49	-29	-75	24
R Calcarine cortex		8.69	18	-68	6
L Lobule VI of cerebellar hemisphere		8.25	-9	-75	-16
L Calcarine cortex		8.12	-4	-78	9
L Inferior temporal gyrus		7.85	-44	-42	-16
L Lobule IV, V of vermis		7.67	-2	-50	-21
L Inferior parietal lobule		7.51	-39	-42	46
L Inferior occipital gyrus		6.76	-42	-78	-8
R Lobule VIII of cerebellar hemisphere		5.80	11	-62	-31
L Precentral gyrus	1458	11.53	-46	-2	36
L Superior frontal gyrus		8.58	-26	-5	59
L Insula		7.98	-32	25	6
L Opercular part of the inferior frontal gyrus		6.06	-52	10	-1
L Triangular part of the inferior frontal gyrus		5.38	-39	28	22
L Supplementary motor area	643	11.73	-4	2	62
R Supplementary motor area		7.40	6	12	49
L Median cingulate gyrus		5.29	-6	12	39
R Superior parietal lobule	550	8.30	21	-65	56
R Middle occipital gyrus		7.60	28	-75	29
R Cuneus		5.31	21	-82	44
R Precentral gyrus	372	7.70	51	0	49
R Superior frontal gyrus		6.79	26	-2	56
R Insula	309	7.58	36	18	9
L Thalamus	193	7.76	-12	-18	6
R Supramarginal gyrus	76	6.34	44	-35	44
R Inferior temporal gyrus	46	6.16	54	-68	-8
L Putamen	39	6.24	-22	2	9
R Thalamus	35	6.41	11	-15	14
R Caudate	25	5.80	16	2	19
L Caudate	23	6.52	-16	-2	19

Note. Local peaks from a contrast represent the comparison of $TP_4 > TP_0$. The fMRI results represent a change in brain activation in the visual LDT (experimental > control). All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

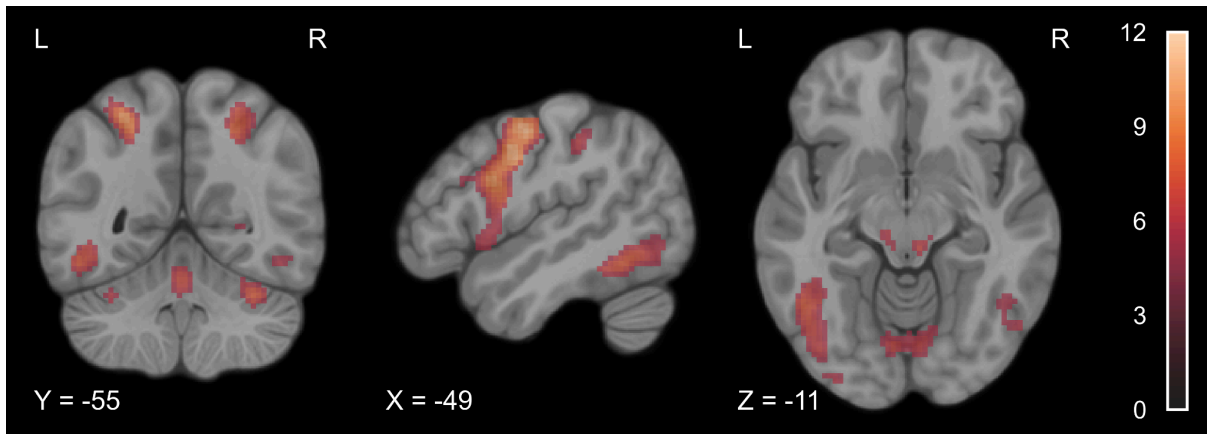


Figure 26. Statistical map of the paired t-test comparison of $TP_4 > TP_0$ for experimental > control contrast in the visual Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

$TP_5 > TP_0$

Three months after ending the Braille course, a paired t-test comparison (TP_5 vs TP_0) revealed that many visual Braille-related activations remained significantly above baseline. Bilateral increases were observed in the calcarine cortex, frontal operculum, precentral gyrus, superior parietal lobule, superior occipital gyrus, and supplementary motor cortex, suggesting the retention of engagement of visual-spatial and motor-linguistic networks.

In the left hemisphere, notable additional activations included the inferior occipital gyrus, inferior temporal gyrus (encompassing the VWFA region), middle frontal gyrus, middle occipital gyrus, supramarginal gyrus, and the thalamus, consistent with a partially sustained reading/language circuit for visually deciphering Braille letters. Meanwhile, on the right, the cerebellar vermis (lobules VI-VII), cerebellar hemisphere, orbital part of the inferior frontal gyrus, and superior frontal gyrus remained more active relative to baseline. These findings indicate that certain bilateral motor-planning, subcortical, and attentional components persisted at follow-up, albeit with some right-hemisphere regions presumably showing reduced involvement compared with the end of training.

Although some right-hemisphere support may have diminished, these results demonstrate lasting neuroplastic changes in both hemispheres, including left-lateralised reading areas (VWFA, inferior frontal gyrus) and bilateral visual-spatial/motor networks. Even without explicit visual Braille practice, participants retained the ability to interpret Braille visually, likely a product of cross-modal transfer from their months of tactile-focused instruction.

Further details regarding peak coordinates and anatomical labels can be found in **Table 23** (**Figure 27**).

Table 23. The comparison of $TP_5 > TP_0$ in the visual Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Precentral gyrus	1275	11.21	-54	0	46
L Opercular part of the inferior frontal gyrus		9.71	-49	8	24
L Insula		7.89	-32	28	4
L Triangular part of the inferior frontal gyrus		5.86	-39	28	22
L Superior parietal lobule	1010	9.33	-26	-62	56
L Middle occipital gyrus		8.04	-29	-75	24
L Inferior parietal lobule		7.40	-39	-42	46
L Supplementary motor area	504	11.64	-4	2	59
R Supplementary motor area		7.07	6	12	49
R Calcarine cortex	491	7.16	18	-70	9
L Calcarine cortex		7.13	-6	-82	6
R Superior occipital gyrus	308	7.39	28	-78	32
R Superior parietal lobule		7.35	21	-65	56
R Insula	180	7.35	34	28	2
R Lobule VI of cerebellar hemisphere	169	8.48	28	-68	-24
L Fusiform gyrus	164	6.69	-42	-52	-11
L Inferior occipital gyrus		5.67	-42	-78	-8
R Lobule VI of cerebellar hemisphere	69	5.98	8	-75	-18
L Thalamus	64	6.78	-12	-15	9
R Superior frontal gyrus	56	6.47	26	-2	54
R Precentral gyrus	29	5.75	51	0	49

Note. Local peaks from a contrast represent the comparison of $TP_5 > TP_0$. The fMRI results represent a change in brain activation in the visual LDT (experimental > control). All the presented results have been thresholded using the FWE correction ($p < 0.05$) together with a cluster extent of 20 voxels and masked with significant voxels from the main effect of time. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

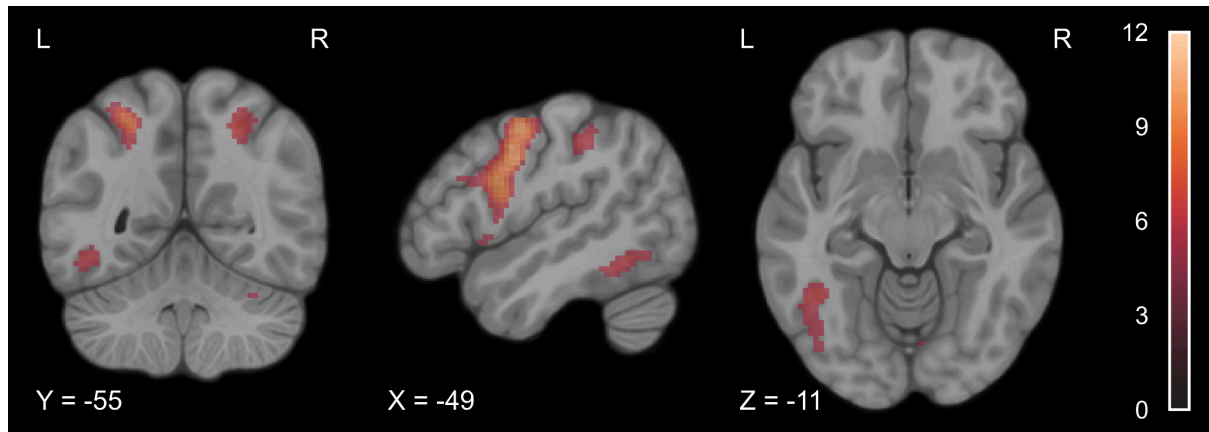


Figure 27. Statistical map of the paired t-test comparison of $TP_5 > TP_0$ for experimental > control contrast in the visual Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

The comparison of all time points during learning

We performed a series of paired t-test comparisons of the experimental > control contrast across multiple time points during Braille learning ($TP_2 > TP_1$; $TP_3 > TP_1$; $TP_4 > TP_1$; $TP_5 > TP_1$; $TP_3 > TP_2$; $TP_4 > TP_2$; $TP_5 > TP_2$; $TP_4 > TP_3$; $TP_5 > TP_3$; $TP_5 > TP_4$). None of these comparisons revealed a significant difference in activity, indicating that the overall pattern of activation for Braille words (relative to control) did not change substantially between these time points.

4.3. Discussion

4.3.1. Study overview and design rationale

This longitudinal investigation examined how the adult brain reorganises while sighted learners acquire Braille, using three parallel lexical decision tasks (LDTs): print (visual alphabet), visual Braille, and tactile Braille, and tracking changes at multiple time points relative to a baseline (TP_0), with a pre-training repetition control to rule out mere test-retest effects. By sampling across early, mid, and late training and including a follow-up after a practice hiatus, the design provides a high-resolution investigation of when and where learning-related changes emerge, rather than inferring plasticity from a single pre-vs-post contrast. This approach addresses gaps in prior work that established cross-modal recruitment of visual and language systems in blind individuals and in sighted Braille readers, but often lacked dense time-course sampling or systematic within-subject tracking across sensory modalities (Amedi et al., 2003; Merabet et al., 2008; Reich et al., 2011; Siuda-Krzywicka et

al., 2016). Framed within contemporary theories of reading and cortical reuse, it also tests predictions from interactive accounts of ventral occipitotemporal function and neuronal recycling that the VWFA becomes tuned to orthographic structure (White et al., 2023) via top-down constraints from language systems and can do so independent of the sensory channel (Cerpelloni et al., 2025; Y.-F. Liu et al., 2023).

4.3.2. Key results

Behaviorally, Braille reading improved relative to baseline in both accuracy and speed. Gains were steeper and earlier for visual Braille than for tactile Braille, compatible with the higher information bandwidth of vision and the serial, effortful nature of tactile decoding. The modest declines observed after a practice break indicate partial forgetting but retained proficiency above baseline, a typical skill-learning profile in which initial gains consolidate yet remain sensitive to disuse (Walsh et al., 2023). The stability of print reading in LDT across matched time points provides an internal benchmark against which Braille-related changes can be interpreted as learning-specific rather than consequences of repetition or scanner habituation.

The print LDT showed no systematic change in brain activity over time, reinforcing that subsequent effects reflect plasticity associated with new literacy rather than global fluctuations. For visual Braille, increases emerged rapidly. Within the first week, bilateral fronto-parietal, supplementary motor, and insular regions were recruited, accompanied by occipital and cerebellar engagement. Such an activation profile is characteristic of domain-general control/attention engaged by novel, effortful tasks (Assem et al., 2020; Shashidhara et al., 2024). Cerebellar recruitment is also consistent with predictive/linguistic contributions during word processing (Mechtenberg et al., 2024). Over the next several weeks, the response expanded to include the VWFA, alongside sustained dorsal stream and language-related prefrontal activity, indicating that orthographic processing was being integrated with top-down linguistic constraints (Yeatman et al., 2024). Many of these visual-Braille increases persisted after a practice hiatus, particularly in left vOTC and fronto-parietal nodes, suggesting that a portion of the reconfigured circuitry had stabilised despite reduced use (Krakauer et al., 2019).

For tactile Braille, early increases prominently involved parietal somatosensory association areas (e.g., inferior parietal lobule/superior parietal lobule), primary sensorimotor cortices, and control regions (supplementary motor area/insula), mirroring the need to explore and encode dot configurations serially through touch (Siuda-Krzywicka et al., 2016). With

continued training, the network broadened to include subcortical structures (thalamus and striatum) and the cerebellum, consistent with cortico-subcortical loops that support sequencing and automatization (Doyon et al., 2018). The VWFA region also became engaged, marking the incorporation of orthographic codes even for tactile input (Reich et al., 2011). As with visual Braille, a substantial subset of tactile-Braille responses remained above baseline after the break, indicating retention of cross-modal reorganisation. These dynamics align with evidence from sensory deprivation and sighted training paradigms showing that occipital and vOTC regions can be recruited for tactile tasks under appropriate conditions, including Braille reading in the congenitally blind and sighted learners (Siuda-Krzywicka et al., 2016; Tian et al., 2023).

4.3.3. Mechanisms of learning to read Braille

Two broad themes emerge from integrating these results with the literature. First, the brain appears to pass through a scaffolding-to-tuning sequence during new literacy: early, bilateral engagement of fronto-parietal control and sensorimotor systems gives way to a more efficient, left-lateralized network that includes VWFA and perisylvian language areas once mapping between form and sound/meaning is established (Price & Devlin, 2011; White et al., 2023). Second, the VWFA can act as a metamodal orthographic hub: in sighted adults, once behaviorally meaningful letter-sound mappings are learned, tactile input recruits VWFA (Siuda-Krzywicka et al., 2016). Parallel evidence from blindness and sensory-substitution shows that “visual” territories can support reading-like computations without vision (Striem-Amit et al., 2012; Tian et al., 2023). After training pauses, VWFA-linked responses remained above baseline, consistent with durable but practice-supported mappings (Krakauer et al., 2019; Matuszewski et al., 2021).

The findings align with a literature-grounded progression from early scaffolding to tuning and efficient retention during new literacy. In the initial week, unfamiliar Braille elicits broad engagement of the multiple-demand control system (dorsolateral prefrontal, dorsal/anterior cingulate, anterior insula, intraparietal/superior parietal), together with modality-specific sensorimotor cortices, consistent with domain-general scaffolding for novel, effortful tasks (Assem et al., 2020; Shashidhara et al., 2024). In parallel, cortico-subcortical learning loops contribute: striatal/basal-ganglia and cerebellar circuits support sequence acquisition and automatization, and higher-order thalamic input modulates learning in goal-directed tactile behaviour (Doyon et al., 2009; La Terra et al., 2022). With repeated practice, pathways linking tactile/visual Braille inputs to VWFA strengthen and orthographic codes emerge;

these are increasingly shaped by top-down predictions from perisylvian language systems: an interactive-processing account verified by task-dependent VWFA-language up-regulation (Saygin et al., 2016; White et al., 2023). Training studies further indicate causal instruction-related changes in the category-selective visual cortex, aligning with the observed rise of VWFA involvement as mappings stabilise (Yeatman et al., 2024). In later/retention phases, processing becomes more focal and left-lateralised (VWFA with perisylvian language regions), with reduced reliance on auxiliary control systems; after practice breaks, responses typically remain above baseline yet slightly attenuated, which can be considered a durable consolidation that still benefits from continued use (Chein & Schneider, 2005; Krakauer et al., 2019). Converging evidence from multiple modalities shows that the VWFA can be co-opted for tactile reading when behaviorally meaningful associations are learned (sighted training) and also engages during Braille use in blindness, which underscores constrained metamodal reuse (Siuda-Krzywicka et al., 2016; Tian et al., 2023).

4.3.4. Limitations, generalizability, and next steps

A pre-training repeat scan and stable print performance rule out scanner habituation, practice effects, and time-of-day influences, indicating that Braille-task changes reflect learning. Nonetheless, early contrasts likely included additional motor/attentional load from slow, serial finger exploration, inflating dorsal and salience activity, which suggests that the early phases of learning result in more domain-general scaffolding rather than language-specific processing (Shashidhara et al., 2024). Due to the limited sample size, a conservative statistical threshold was employed with whole-brain corrections (FWE $p \leq 0.05$, cluster extent ≥ 20). However, this approach may under-detect subtle late-phase refinement (Button et al., 2013; Lieberman & Cunningham, 2009). Generalizability of presented results is limited: sighted adult learners differ from congenitally blind readers; similar loci (e.g. VWFA) do not imply identical computations, as blindness induces occipital language functions and certain fine-grained VWFA tuning properties may depend on visual experience (Bedny et al., 2011; Kim et al., 2017). Having all these arguments in mind, future work should prioritise larger sample sizes. Future studies could more densely sample the earliest days to test whether frontoparietal demand peaks precede VWFA tuning. Furthermore, they could manipulate practice *dose* to probe coupling between VWFA and perisylvian language regions, or use causal perturbation to test the engagement of specific regions across stages of the learning process (Gaillard et al., 2006; Hirshorn et al., 2016).

5. Shared and modality-specific reading networks in print and Braille

What are the brain networks engaged in tactile and visual Braille reading? Which regions are involved in Braille word processing, regardless of the presentation domain?

In sighted people, the Braille alphabet can be learned using both vision and touch. Contrasting visual and tactile Braille-related activity could help identify which regions of the reading network are specifically engaged in tactile reading. Previous research involving the same group of sighted Braille teachers has demonstrated that visual Braille reading, which lacks natural line junctions, is significantly less efficient than reading scripts such as Cyrillic. Even with prior visual Braille knowledge, reading was slower and more error-prone than in the Cyrillic alphabet learning group after just three months of learning (Bola, Radziun, et al., 2017). Although tactile and visual reading have been tested using fMRI methodology before (Siuda-Krzywicka et al., 2016), no direct comparison has been computed. This highlights the need for such a comparison to understand the specific mechanisms engaged in tactile Braille reading, preferably in naive people with no prior Braille knowledge.

5.1. Aims, research questions, and predictions

This within-subject study was designed to identify which components of the reading network are shared across print, visual Braille, and tactile Braille, and which remain modality-specific. The central goal was to test for overlap in reading-related network recruitment while also characterising differences associated with visual and tactile input.

It addressed the following research questions:

1. Which regions are recruited across all three lexical decision tasks: print, visual Braille, and tactile Braille?
2. Which regions are shared by the two Braille tasks but not by print reading?
3. Which regions show stronger task involvement that is more specific to visual Braille?
4. Which regions show stronger task involvement that is more specific to tactile Braille?

The main predictions were as follows. A shared left-lateralised reading-related core was expected across all three tasks, especially in the inferior frontal and ventral occipitotemporal cortex. Relative to print, Braille was expected to recruit an expanded network involving parietal, dorsal occipital, cerebellar, and subcortical regions, reflecting additional demands on spatial, attentional, and sequencing processes. Visual Braille was expected to show stronger occipital and visual-attention involvement, whereas tactile Braille was expected to show

stronger sensorimotor, parietal, supplementary motor, and cerebellar recruitment. Shared recruitment was interpreted as overlap in reading-related network engagement rather than as evidence of identical computations across modalities.

5.2. Results

5.2.1. Sensory independent networks

A conjunction analysis spanning all three Lexical Decision Tasks (print, visual Braille, and tactile Braille) revealed a set of regions consistently active across modalities (see **Table 24** and **Figure 28**). In the left hemisphere, a large cluster centred on the inferior frontal gyrus (orbital, opercular, and triangular parts) emerged, along with adjacent areas in the precentral and postcentral gyri. This cluster underscores the phonological, articulatory, and motor-planning components that appear to be shared across all reading forms, whether the input is visual (print or Braille) or tactile. Additionally, a distinct peak in the left inferior temporal gyrus (extending into the middle temporal gyrus) points to a VWFA that remains active across these tasks.

In the right hemisphere, a corresponding frontal-motor cluster in the inferior frontal gyrus (triangular and opercular parts) and the insula was consistently engaged, suggesting bilateral support for cognitive control and salience/attentional mechanisms. The right supplementary motor area also appeared in conjunction, indicating that high-level motor sequencing or domain-general executive processes may be recruited for reading across multiple sensory modalities. Lastly, the left medial superior frontal gyrus exhibited conjunctive activity, implicating midline frontal regions in reading-related decision-making or control.

These sensory-independent regions, encompassing bilateral inferior frontal gyrus, motor/insular cortex, and left temporal/ventral-occipitotemporal areas, demonstrate that the brain leverages a shared reading circuitry irrespective of input modality. Whether participants saw traditional letters (print), viewed Braille letters visually, or felt Braille by touch, this conjunction analysis highlights a shared frontotemporal network that subserves the linguistic, phonological, and motor components of reading.

Table 24. The conjunction of activity in Lexical Decision Tasks.

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Orbital part of the inferior frontal gyrus	1661	11.34	-44	22	-6
L Opercular part of the inferior frontal gyrus		10.37	-46	10	26
L Triangular part of the inferior frontal gyrus		9.43	-52	35	6
L Precentral gyrus		6.33	-44	-2	42
L Postcentral gyrus		5.65	-54	-8	49
R Triangular part of the inferior frontal gyrus	655	8.51	54	18	24
R Opercular part of the inferior frontal gyrus		7.86	44	8	26
R Insula		7.85	36	25	-4
R Supplementary motor area	508	9.25	6	20	54
L Medial part of the superior frontal gyrus		8.22	-4	30	52
L Inferior temporal gyrus	276	12.83	-46	-40	-16
L Middle temporal gyrus	63	6.91	-54	-45	6

Note. Local peaks from a contrast represent the main effect of condition in all LDTs. X, y, and z are MNI coordinates. All the presented results have been thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

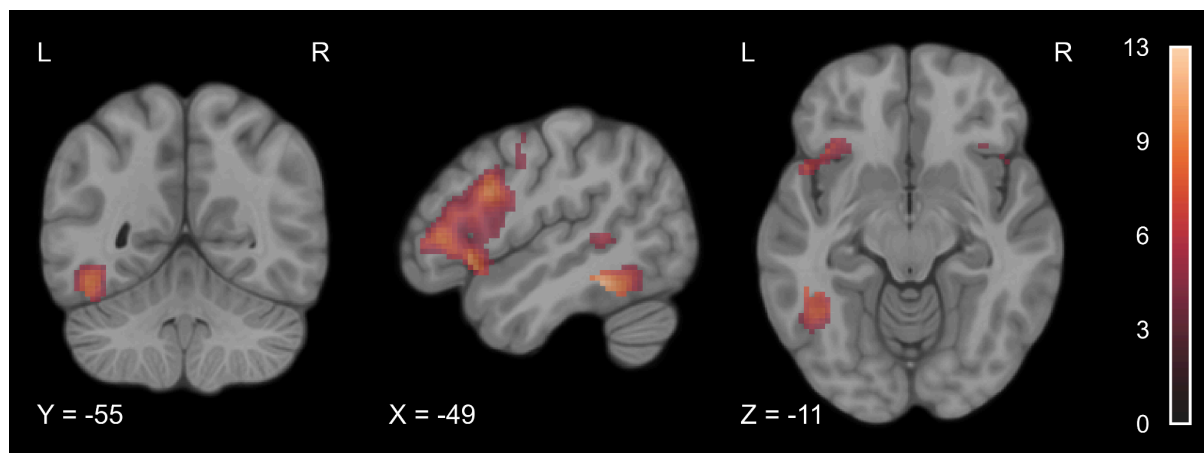


Figure 28. Statistical map of the conjunction of activity for experimental > control contrast in the tactile Braille, visual Braille and print Lexical Decision Tasks. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

5.2.2. Braille-general activations

A conjunction of the visual and tactile Braille Lexical Decision Tasks, excluding any active areas for print LDT, revealed broad, bilateral engagement in fronto-parietal, subcortical, and cerebellar networks (see **Table 25** and **Figure 29**). In the left hemisphere, a large cluster spanned the supplementary motor area, inferior frontal gyrus (opercular and triangular parts), pre- and postcentral gyri, anterior cingulate, insula, inferior temporal gyrus, and thalamus, along with additional peaks in the caudate and cerebellar lobule VI. These results underscore

extensive motor-linguistic and subcortical involvement specifically associated with Braille reading modalities (both touch and visual), separate from traditional print processing.

A corresponding set of right-hemisphere areas was likewise more active for Braille than for print, including the opercular and triangular inferior frontal gyrus, middle frontal gyrus, precentral gyrus, and insula, indicating a bilateral frontal network underpinning Braille-related phonological or executive demands. Further right parietal engagement included the inferior and superior parietal lobules, angular gyrus, and superior occipital gyrus, reflecting visuospatial attention or shape-based decoding that is uniquely pronounced in Braille tasks. The cerebellum was also involved bilaterally (lobule VI and lobule VIII of the vermis), consistent with coordinated finger scanning (tactile) and/or attention to dot patterns (visual).

In short, these Braille-specific regions, spanning motor-linguistic circuitry, parietal-occipital areas, and subcortical nodes, constitute a shared substrate for processing Braille via touch and sight, distinct from the print-based reading system.

Table 25. The Braille-general activity in Lexical Decision Tasks.

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Supplementary motor area	10903	18.20	-4	2	59
R Lobule VI of cerebellar hemisphere		17.15	31	-70	-26
L Triangular part of the inferior frontal gyrus		16.57	-46	28	24
L Precentral gyrus		16.55	-54	0	46
L Inferior temporal gyrus		15.47	-49	-60	-8
L Postcentral gyrus		14.99	-49	-8	52
L Opercular part of the inferior frontal gyrus		14.19	-49	12	2
L Thalamus		14.04	-14	-15	9
L Insula		13.75	-29	22	6
L Lobule VI of cerebellar hemisphere		13.30	-26	-70	-26
L Caudate		13.23	-16	5	14
L Anterior cingulate gyrus		12.99	-6	5	29
L Inferior parietal lobule	2156	16.49	-29	-75	42
L Superior parietal lobule		13.59	-26	-65	62
R Middle frontal gyrus		9.60	46	2	54
R Insula		9.13	34	18	-6
R Triangular part of the inferior frontal gyrus		8.12	46	20	26
R Orbital part of the inferior frontal gyrus		7.85	31	25	-11
R Putamen		6.79	34	2	-1
R Precentral gyrus		6.67	41	0	46
R Opercular part of the inferior frontal gyrus	2025	14.63	51	8	26
R Superior frontal gyrus		11.99	24	-2	54
R Inferior parietal lobule	1710	14.45	38	-45	49
R Supramarginal gyrus		13.93	44	-35	42
R Superior occipital gyrus		13.37	28	-65	36
R Angular gyrus		12.22	28	-58	44
R Superior parietal lobule		11.71	21	-68	54
L Supramarginal gyrus	70	7.62	-62	-42	24
L Lobule VIII of cerebellar hemisphere	25	8.80	-14	-62	-48

Note. Local peaks from a contrast represent the main effect of condition in the visual and tactile Braille LDT. The voxels active in the print LDT are excluded. X, y, and z are MNI coordinates. All the presented results have been thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

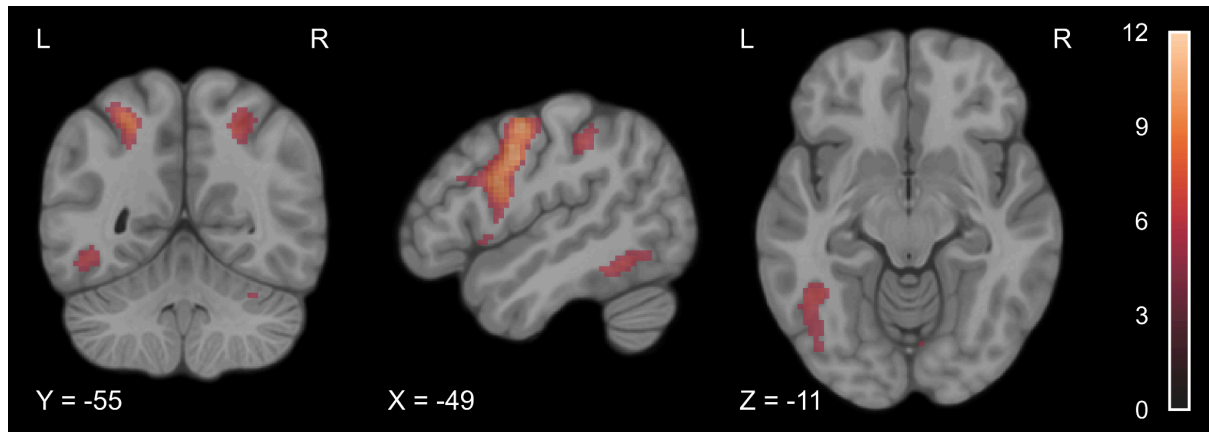


Figure 29. Statistical map of Braille-general activations in the Lexical Decision Tasks in the main effect of condition (experimental > control). The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

5.2.3. Visual Braille

A large bilateral occipital cluster emerged as uniquely engaged by visual Braille, spanning the middle and inferior occipital gyri, calcarine cortex, fusiform gyrus, and (on the right) extending into the inferior temporal gyrus. (See **Table 26** and **Figure 30**). This pattern underscores a visual-perceptual processing route that is distinctly used for Braille letter shapes when presented visually. Several right frontal areas also displayed selective involvement, namely the superior/middle frontal gyri, precentral gyrus, and the opercular/triangular parts of the inferior frontal gyrus, pointing to a right-lateralised executive or motor-planning dimension for decoding unfamiliar visual stimuli. Similarly, the anterior cingulate (including the median cingulate gyrus) and the insular cortex were more active on the right, suggesting heightened attentional or conflict-monitoring resources allocated exclusively to visual Braille. On the left side, a smaller but notable set of frontal peaks (e.g., middle and superior frontal gyri, triangular inferior frontal gyrus) also appeared, together with pre- and postcentral involvement, implying that linguistic or articulatory processes may still be partially lateralised to the left, even for visually presented Braille. Further subcortical and cerebellar contributions included several lobules in the cerebellar vermis and hemispheres (Crus I/II, lobule III/VIII), consistent with sensorimotor coordination and error-correction mechanisms often triggered by novel orthographic input.

Overall, these results highlight a distinct set of networks dedicated to visual Braille alone, engaging visual-occipital pathways, right-frontal attentional and motor-executive systems, and modest left-frontal-motor components, demonstrating how the brain processes Braille dot

configurations by sight differently than it does either print or tactile versions of the same script.

Table 26. The activity specific to visual Braille reading in the Lexical Decision Task.

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Middle occipital gyrus	5488	18.85	-29	-80	19
R Middle occipital gyrus		16.19	31	-78	26
L Inferior occipital gyrus		16.07	-36	-88	-6
R Calcarine cortex		15.79	14	-70	12
L Calcarine cortex		15.08	-2	-78	9
L Fusiform gyrus		14.52	-39	-70	-14
R Superior occipital gyrus		14.20	26	-80	36
R Inferior occipital gyrus		13.96	44	-65	-11
R Inferior temporal gyrus		12.32	51	-70	-8
R Superior frontal gyrus	713	15.68	16	8	64
R Middle frontal gyrus		12.77	36	35	34
R Precentral gyrus		12.25	36	2	32
R Supplementary motor area		11.48	8	15	62
R Triangular part of the inferior frontal gyrus		9.83	36	28	26
R Medial part of the superior frontal gyrus		6.95	8	25	56
R Lobule III of vermis	531	8.55	6	-38	-18
R Lobule IX of vermis		7.26	1	-52	-34
L Lobule III of vermis		7.20	-2	-42	-14
L Lobule VIII of cerebellar hemisphere		7.10	-14	-60	-38
L Lobule III of cerebellar hemisphere		7.04	-4	-40	-21
R Lobule IX of cerebellar hemisphere		7.03	4	-45	-44
R Median cingulate gyrus	197	10.39	8	35	34
R Anterior cingulate gyrus		8.75	11	38	24
R Medial part of the superior frontal gyrus		8.75	11	30	44
L Anterior cingulate gyrus		6.52	-6	25	24
R Opercular part of the inferior frontal gyrus	152	12.27	41	12	4
R Insula		11.12	36	15	12
R Orbital part of the inferior frontal gyrus		8.16	48	20	-8
R Triangular part of the inferior frontal gyrus		7.43	56	20	9
L Middle frontal gyrus	128	9.06	-34	40	24
L Triangular part of the inferior frontal gyrus		8.73	-36	32	26
L Superior frontal gyrus	44	10.01	-16	10	62
L Middle frontal gyrus		8.02	-24	8	52
R Caudate	38	6.40	14	20	2
L Insula	33	11.02	-36	12	12
L Opercular part of the inferior frontal gyrus		5.31	-44	8	12
L Precentral gyrus	26	10.52	-39	-10	44
L Postcentral gyrus		8.31	-46	-8	36
L Crus II of cerebellar hemisphere	25	9.62	-39	-62	-46
L Crus I of cerebellar hemisphere		8.27	-46	-65	-36

L Insula	7.82	-36	15	-11
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Note. Local peaks from a contrast represent the main effect of condition in the visual Braille LDT. The voxels active in other LDTs are excluded. X, y, and z are MNI coordinates. All the presented results have been thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

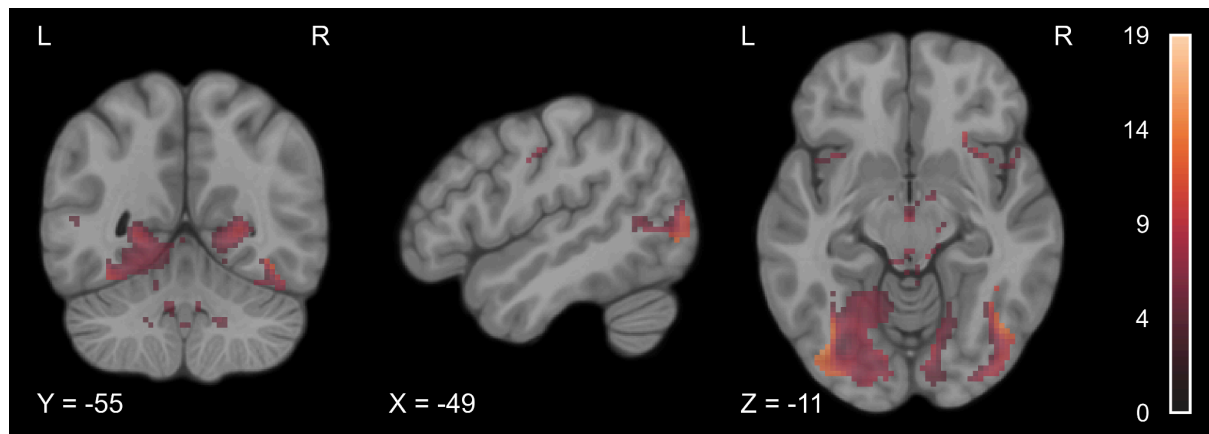


Figure 30. Statistical map of visual Braille-specific activations in the Lexical Decision Tasks in the main effect of condition (experimental > control). The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

5.2.4. Tactile Braille

A broad bilateral pattern emerged for tactile Braille reading, concentrated in sensorimotor and parietal-frontal circuits (See **Table 27** and **Figure 31**). In the left hemisphere, prominent clusters spanned the pre- and postcentral gyri, supplementary motor area, superior and inferior parietal lobules, and the angular/supramarginal gyri, consistent with the somatosensory and motor aspects of Braille exploration (finger scanning). Likewise, left-lateralised subcortical areas, such as the putamen, thalamus, and insula, showed uniquely tactile involvement, indicating deeper integration of somatosensory signals with motor-linguistic processing. The left inferior temporal gyrus and fusiform gyrus also appeared, suggesting that tactile-based orthographic or higher-order linguistic encoding can extend into the ventral occipitotemporal territory.

On the right, sensorimotor features were similarly strong. The right postcentral and precentral gyri, supplementary motor area, and superior parietal lobule signalled involvement in fine motor control of fingertip movements. Additional subcortical-cerebellar peaks, including the right and left cerebellar hemispheres (lobule VI/Crus I/II) and parts of the vermis, highlight coordination and timing mechanisms tailored to tactile scanning. Frontal contributions (e.g., right orbital and opercular inferior frontal gyrus, middle frontal gyrus) further suggest a

bilateral executive-attentional component unique to tactile decoding, distinct from the circuits engaged by visual or print reading.

Overall, these tactile-specific regions emphasise the motor-somatosensory nature of Braille reading by touch and dedicated subcortical and cerebellar resources that handle precise finger exploration and cross-modal integration for Braille's spatially distributed letterforms.

Table 27. The activity specific to tactile reading in the Lexical Decision Task.

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Postcentral gyrus	1596	13.66	-46	-35	56
L Precentral gyrus		13.46	-44	-12	59
L Inferior parietal lobule		13.44	-52	-28	46
L Superior parietal lobule		10.02	-34	-52	64
L Supplementary motor area		9.96	-4	-5	54
L Supramarginal gyrus		8.31	-54	-28	32
R Supplementary motor area		7.76	4	-5	62
L Superior frontal gyrus		7.52	-16	-10	76
R Posterior cingulate gyrus		7.07	6	-38	26
L Median cingulate gyrus		6.99	-4	-8	32
R Postcentral gyrus	665	14.30	51	-22	46
R Supramarginal gyrus		9.59	51	-30	39
R Superior parietal lobule		8.17	24	-58	66
R Precentral gyrus		6.51	56	-8	46
L Putamen	284	11.30	-26	-5	2
L Insula		8.51	-39	-2	9
R Lobule VI of cerebellar hemisphere	252	13.20	26	-55	-24
R Lobule IV, V of vermis		7.64	4	-50	-6
R Superior frontal gyrus	151	11.92	31	-10	59
R Putamen	141	8.51	26	5	4
R Pallidum		7.34	24	-5	6
R Insula		6.07	38	0	6
R Orbital part of the middle frontal gyrus	55	7.57	28	40	-16
R Orbital part of the inferior frontal gyrus		7.18	36	35	-6
L Triangular part of the inferior frontal gyrus	54	8.89	-46	45	2
L Middle frontal gyrus		6.93	-39	50	6
L Lobule VI of cerebellar hemisphere	52	10.29	-29	-52	-26
L Thalamus		8.75	-16	-25	4
L Fusiform gyrus		5.69	-32	-40	-24
L Inferior temporal gyrus	50	9.67	-52	-50	-8
L Inferior parietal lobule	48	8.76	-34	-72	39
L Angular gyrus		7.52	-36	-62	42
R Triangular part of the inferior frontal gyrus	47	8.67	51	35	6
R Middle frontal gyrus		5.02	36	42	6
R Crus I of cerebellar hemisphere	39	7.35	16	-78	-28
R Crus II of cerebellar hemisphere		6.60	38	-68	-41

L Orbital part of the inferior frontal gyrus	29	6.79	-26	28	-18
L Medial part of the superior frontal gyrus	27	6.83	-6	35	34
R Precentral gyrus	20	8.63	61	5	29
R Rolandic operculum		6.53	61	10	12

Note. Local peaks from a contrast represent the main effect of condition in the tactile Braille LDT. The voxels active in other LDTs are excluded. X, y, and z are MNI coordinates. All the presented results have been thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

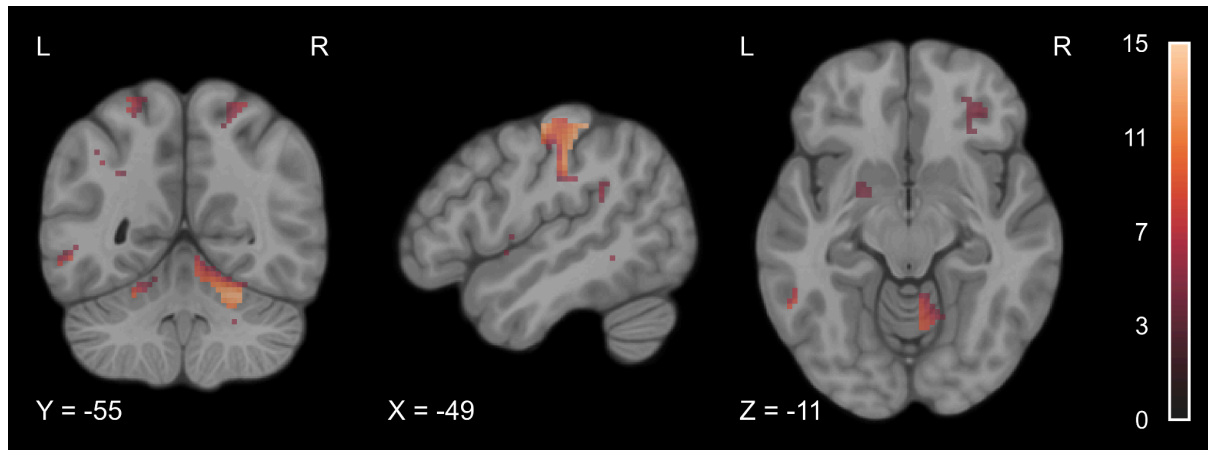


Figure 31. Statistical map of tactile Braille-specific activations in the Lexical Decision Tasks in the main effect of condition (experimental > control). The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

5.3. Discussion

5.3.1. Study overview and design rationale

The goal of this experiment was to identify sensory-independent components of the reading/language network, those shared across tactile Braille, visual Braille, and print, and to dissociate sensory-dependent, modality-specific components within the same individuals (Y.-F. Liu et al., 2023; Tian et al., 2023). By leveraging within-subject fMRI contrasts in sighted adults trained in Braille, this design minimises inter-individual variance and isolates modality effects that are often conflated in between-group studies of blind readers or single-modality paradigms (Chauhan et al., 2024; J. Li et al., 2024). This fills a gap in the literature, in which most prior work has examined a single modality or blindness, leaving open how a sighted adult's reading system incorporates a novel tactile script while maintaining the canonical reading architecture (Reich et al., 2011; Siuda-Krzywicka et al., 2016; Striem-Amit et al., 2012). The within-subject, three-condition comparison allows direct

tests of metamodal versus modality-bound organisation of the reading system in typical sighted brains (Dzięciel-Fivet et al., 2021; Kim et al., 2017).

5.3.2. Key results

5.3.2.1. Metamodal network

The conjunction analysis identified a shared left-lateralised reading-related network across print, visual Braille, and tactile Braille, centred on the left inferior frontal gyrus (pars opercularis/triangularis), adjacent premotor cortex, and left ventral occipitotemporal cortex, including VWFA. IFG engagement across all three tasks is consistent with phonological and lexical selection demands during silent lexical decision, irrespective of the input route (Uddén et al., 2022; Uno et al., 2025). Premotor involvement may reflect covert articulation or inner speech, while bilateral insular and supplementary motor contributions likely index task-general salience, response selection, and executive support shared across conditions (Chung et al., 2023; Schimmelpfennig et al., 2023; Silva et al., 2022; Williams et al., 2022). Crucially, overlap in left vOTC, including the VWFA region, across tasks supports shared recruitment of a reading-related core. Still, it should not be treated as proof of identical computations across print and Braille or of complete modality independence. The present conjunction shows that once orthographic input is behaviourally meaningful, both visual and tactile formats can engage left-lateralised regions typically implicated in orthographic-to-linguistic mapping. This interpretation is consistent with evidence that both connectivity and task demands shape VWFA recruitment, and that its engagement can be modulated by top-down linguistic constraints (Dębska et al., 2023; Yablonski et al., 2024). Thus, within-subject comparisons in sighted Braille learners support a division of labour between shared reading-related recruitment and condition-specific input interfaces. Print, visual Braille, and tactile Braille converge on the left IFG and vOTC. In contrast, the broader Braille networks additionally recruit parietal, occipital, cerebellar, and subcortical systems, likely reflecting perceptual, spatial, sensorimotor, and sequencing demands. The observed overlap therefore supports a restricted metamodal claim: shared recruitment of part of the reading network across input routes, rather than a claim of fully modality-free or computationally identical processing (Reich et al. 2011; Striem-Amit et al. 2012; Tian et al. 2023).

5.3.2.2. Braille-general activations

The intersection of the two Braille modalities (excluding print) revealed a broader bilateral network, encompassing right inferior frontal gyrus/anterior insula, bilateral superior/inferior parietal lobules, dorsal occipital regions, cerebellum, and subcortical structures (thalamus, caudate). This profile suggests elevated demands on spatial attention, working memory, and cognitive control when processing an effortful/unfamiliar orthographic code relative to an overlearned print code (Chrabaszcz et al., 2025). The involvement of the cerebellum and basal ganglia in Braille-general maps is consistent with their roles in sequencing and automatization during the acquisition of novel skills (Fleischer et al., 2023; Roth & Ding, 2024). Convergent findings in sighted Braille learners indicate widespread recruitment and strengthened cross-modal connectivity after training, underscoring a large-scale reconfiguration that extends beyond the visual network alone (Perdue et al., 2022).

5.3.2.3. Visual Braille-specific

Exclusive maps for visual Braille identified bilateral occipital cortices (calcarine/lingual and middle/inferior occipital gyri) and ventral occipitotemporal regions engaged only by visually presented Braille. This pattern reflects obligatory visual entry through early- to mid-level visual areas and onward transmission to VWFA when symbols are perceived (Lerma-Usabiaga et al., 2018). More extensive dorsal parietal recruitment for visual Braille than print likely indexes the atypical spatial analysis demands of dot-matrices without the contour junctions that facilitate fluent letter identification in typical scripts, consistent with behavioural inefficiency for visual Braille (Bola, Radziun, et al., 2017). Despite these additional perceptual demands, visual Braille still engages the downstream left-hemisphere reading network (inferior frontal gyrus-VWFA), indicating convergence once orthography is decoded (Cerpelloni et al., 2025).

5.3.2.4. Tactile Braille-specific

Exclusive maps for tactile Braille highlighted the left postcentral gyrus (S1, finger representation), superior parietal lobule, supplementary motor area, cerebellum, and basal ganglia, reflecting tactile encoding, spatial exploration, and sequential finger movements that are unique to reading by touch. S1 and dorsal parietal engagement is a hallmark of Braille-by-touch and is reported both in proficient blind readers and in sighted Braille learners (Y.-F. Liu et al., 2023; Matuszewski et al., 2021). Enhanced involvement of putamen/caudate and lobule VI/IX of the cerebellum is consistent with striato-cerebellar loops that support habit formation, chunking, and timing during emerging skilled tactile

reading (J. Li et al., 2024; Roth & Ding, 2024). Unlike congenitally blind readers, who often recruit the primary visual cortex during Braille and other nonvisual language tasks, sighted learners did not show unique V1 recruitment beyond the shared core, suggesting that the early occipital cortex remains visually dedicated in sighted adults (Duymuş et al., 2024; Tian et al., 2023). At the same time, the VWFA likely serves as the connectivity-constrained hub linking decoded orthography to language systems (Dębska et al., 2023; Yablonski et al., 2024).

The sensory-independent core we observed (inferior frontal gyrus-VWFA plus bilateral executive support) aligns with converging evidence that the VWFA implements orthographic processing independently of visual experience, provided that inputs are transformed into letter-like codes upstream (Reich et al., 2011; Striem-Amit et al., 2012). Within VWFA, functional/structural constraints favour convergence across scripts, with subregional specialisations shaped by experience and task demands (Lerma-Usabiaga et al., 2018). However, the degree and profile of VWFA selectivity vary with developmental visual experience. In blind readers, the VWFA responds to Braille yet exhibits altered gradients and broader linguistic sensitivity relative to sighted individuals (Tian et al., 2023). Visual Braille-specific occipital/parietal pattern is expected from feed-forward visual entry to VWFA with additional dorsal attention demands when symbol features are atypical, as in dot-matrices (Cerpelloni et al., 2025). In parallel, tactile-Braille-specific S1-parietal-fronto-occipital recruitment supports active, sequential touch, with orthography-specific coding in the posterior parietal cortex and a predominant top-down flow of information from the inferior frontal cortex to the lateral occipital cortex during natural Braille reading (Wang et al., 2024). Training studies in sighted adults further show that strengthening occipito-temporal involvement is functionally relevant: perturbing VWFA disrupts Braille performance (Siuda-Krzywicka et al., 2016). Finally, blind and sighted direct comparisons indicate that beyond sensory entry points (V1 vs S1), written language converges on similar high-level systems with group-specific nuances; recent fMRI and chronometric TMS studies demonstrate similar computational hierarchies for reading and speech in the occipital cortex across groups (Matuszewski et al., 2025).

A parsimonious account consistent with results from within-subject data is that modality-specific input interfaces (occipital V1 for visual Braille; S1-parietal pathways for tactile Braille) deliver orthographic information to a modality-independent core comprising VWFA for orthographic identity and left inferior frontal gyrus/premotor and temporo-parietal

areas for phonological/lexical access (Vin et al., 2024). Top-down predictions from inferior frontal gyrus/temporal language systems interact with VWFA to sharpen orthographic representations regardless of input modality, yielding similar engagement of the core during visual Braille and tactile Braille once symbols are identified as letters (White et al., 2023). Early in learning, scaffolding networks, right frontal-parietal control and subcortical-cerebellar loops are co-opted to manage effortful exploration and sequencing, particularly for Braille, and are expected to recede with automatisisation (Turker et al., 2025). In sighted adults, intact visual experience biases the system toward recruiting the VWFA as a common orthographic hub, while primary visual cortex remains largely modality-bound for reading (Dębska et al., 2023; Seydell-Greenwald et al., 2023). By contrast, in blindness, the VWFA's linguistic role broadens, and canonical orthographic gradients are altered (Paczyńska et al., 2025).

Several features of the design and analysis increase interpretability. First, within-subject contrasts are conducted across tactile Braille, visual Braille, and print to examine differences in anatomy and strategy, and to isolate modality effects at matched task demands. Second, the observed pattern of known-network engagement provides face validity: IFG-VWFA coupling for orthography/lexical access (Dębska et al., 2023; Yablonski et al., 2024), dorsal attention for top-down orienting (Alves et al., 2022; Tosoni et al., 2023), and salience/executive systems for control/switching (Seeley, 2019). Remaining caveats include possible difficulty mismatches. Because Braille (visual and tactile) was less automated than print, the multiple-demand/fronto-parietal network would be expected to scale up with difficulty (T. Wen & Egner, 2023) and then recede with practice as networks reconfigure (Finc et al., 2020). Early effort may also recruit basal ganglia and cerebellar loops that support sequence learning (Bostan & Strick, 2018), so the Braille-general expansion likely reflects both modality and proficiency. The lack of a tactile Braille-specific effect in V1 does not rule out occipital responses to touch. In sighted adults, the early visual cortex is predominantly visual, with orthographic processing centred in VWFA (White et al., 2023). Small top-down or multisensory influences on V1 can still occur. For example, spoken language responses in sighted V1, so a null V1 result for tactile Braille should not be over-interpreted (Seydell-Greenwald et al., 2023).

Within-subject comparisons in sighted Braille learners reveal a division of labour in the reading brain: a modality-invariant core (left inferior frontal gyrus and VWFA, with bilateral executive support) that subserves orthographic-to-linguistic mapping across tactile Braille,

visual Braille, and print, and modality-specific interfaces (V1-occipital for visual Braille; S1-parietal, supplementary motor area, basal ganglia, cerebellum for tactile Braille) that transform sensory input into an abstract orthographic code for the core. The Braille-general expansion relative to print likely reflects added perceptual, spatial-attentional, and sequencing demands during symbol parsing (Janacsek et al., 2020; Tong et al., 2025). At the same time, the observed convergence onto the left-lateralised language network underscores the system's capacity to implement orthography independent of input modality, consistent with VWFA engagement in Braille and print (Tian et al., 2023). These findings motivate the following subsection on implicit tactile reading: if tactile Braille engages the same core network during explicit tasks, does incidental exposure to Braille patterns (without an instruction to read) also recruit this circuitry in trained learners more than in untrained controls? The mixed-design analysis tests this by contrasting learners with passive controls under tasks that do not require reading per se, to assess whether the modality-independent core is triggered automatically in the tactile domain (Cohen et al., 2021; Thuy et al., 2004).

6. Automatic tactile reading-related engagement in Braille learners

Previous research with sighted Braille learners has focused mainly on explicit reading or simple tactile pattern recognition tasks. While invaluable for understanding cross-modal plasticity, these tasks overlook that in everyday life, much of the interaction between sighted individuals and reading occurs without conscious effort, as when reading a book or subtitles while watching a movie (Ross & Kowler, 2013). This form of reading can be defined as implicit. Studies have demonstrated that implicit reading can induce significant activity similar to that observed in explicit reading tasks. For instance, even when subjects are instructed to perform a nonlinguistic visual feature detection task, the presence of words or pseudowords activates a widespread neuronal network that aligns with areas of the reading network (Price et al., 1996; Thuy et al., 2004). This suggests that the brain processes words beyond the task's functional demands, highlighting the underlying mechanisms that support implicit reading. However, to our knowledge, no one has tested whether implicit reading in the tactile domain can induce a different functional response in the brain. With the acquisition of linguistic context for the Braille symbols, such implicit reading could also emerge even in a non-linguistic task. Thus, activation of regions in the reading network in response to tactile Braille stimulation, without an overt linguistic task, would further support the multimodal and modality-independent nature of the brain areas involved in reading.

By incorporating a mixed design, we can evaluate changes in activity throughout the experimental period for both groups - the experimental (learning) group, for which the task possibly tracks implicit reading and symbol detection, and the control (passive) group, for which the task has no reading component, but a detection component remains present.

6.1. Aims, research questions, and predictions

This mixed-design study tested whether Braille learning leads to automatic, reading-relevant neural engagement during a non-linguistic tactile task. Using the 6-dot detection task, the study asked whether incidental exposure to embedded Braille words would differentially engage the brains of Braille learners and passive controls, despite similar overt task demands. It addressed the following research questions:

1. Do Braille learners and passive controls differ in brain activation during the 6-dot detection task?

2. Are any group differences present in reading-relevant regions, especially left inferior frontal and ventral occipitotemporal/fusiform cortex?
3. Do group differences also involve somatosensory-motor, parietal, supplementary motor, subcortical, and cerebellar regions that could support tactile scanning, sequencing, and emerging automaticity?
4. Do any neural group differences change systematically across repeated sessions, or do they mainly reflect a stable consequence of Braille experience?
5. Can any neural group differences be interpreted independently of overt task performance, given that the task itself does not require explicit reading?

The main predictions were as follows. Braille learners were expected to show greater activation than passive controls in reading-relevant and sensorimotor networks during the 6-dot detection task, even though behavioural performance remained similar between groups. These effects were expected to involve the left inferior frontal cortex, ventral occipitotemporal/fusiform regions, parietal attention areas, supplementary motor cortex, thalamostriatal structures, and cerebellum. At the same time, because the task also includes tactile scanning, somatosensory attention, and motor routine, any learner–control difference was interpreted as automatic reading-relevant engagement rather than as a process-pure measure of implicit reading.

6.2. Results

6.2.1. Behavioural results

6.2.1.1. On-site Braille reading tests

We employed a 6 (time) x 2 (group) mixed ANOVA to analyse the behavioural data (number of correctly detected 6-dots) in the DD6 task.

6.2.1.2. Main effect of time

Only the effect of time has reached statistical significance, $F(2.4, 81.54) = 7.12$; $p < 0.001$. We observed a statistically significant increase in the number of correctly detected 6-dots in the DD6 task. The experimental task showed higher accuracy at TP₁, TP₂, TP₃, TP₄, and TP₅ than at TP₀. Additionally, TP₃ had higher correctness than TP₁ (**Table 28**).

Table 28. Post-hoc comparisons between time points in the number of correctly detected stimuli in the 6-dots detection task.

Time point	<i>M</i>	<i>SD</i>	TP ₀	TP ₁	TP ₂	TP ₃	TP ₄
TP ₀	81.28	14.46					
TP ₁	88.36	11.39	0.002				
TP ₂	89.29	9.37	< 0.001	0.64			
TP ₃	91.78	8.26	< 0.001	0.003	0.4		
TP ₄	88.89	9.44	0.002	1	1	0.24	
TP ₅	87.85	11.93	0.03	1	1	0.25	1

Note. TP₀ = Pre-test (On the day of the course), TP₁ = One week into the course, TP₂ = Six weeks into, TP₃ = Three months into, TP₄ = Seven months into, TP₅ = Follow-up (Three months after the end of the course). *p* values with Bonferroni correction for multiple comparisons.

6.2.1.3. Main effect of group, time and group interaction

We observed no significant effect of group [$F(1, 34) = 3.20$; $p = 0.08$] and group and time interaction [$F(2.4, 81.54) = 0.75$; $p = 0.50$]. These results indicate no behavioural differences in DD6 between the Braille learning group and the passive controls.

6.2.2. fMRI results

We analysed fMRI data collected during the DD6 task to examine whether the reading network is involved during implicit Braille reading.

6.2.2.1. Main effect of group

Compared to the passive control group, Braille-trained participants showed more extensive activation in a wide range of cortical and subcortical structures (see **Table 29** and **Figure 32**). Bilateral parietal-frontal sensorimotor networks were strongly engaged, encompassing the pre- and postcentral gyri, supramarginal gyrus, inferior and superior parietal lobules, and the supplementary motor area, all of which are consistent with enhanced tactile attentional resources, motor planning, or heightened somatosensory integration.

On the left side, peaks spread across the paracentral lobule, insula, inferior frontal gyrus (opercular and triangular parts), and subcortical areas (putamen, thalamus), reflecting the Braille learners' increased reliance on, or adaptation of, sensorimotor-linguistic pathways during tactile exploration. Similarly, the right hemisphere exhibited more substantial involvement of frontoparietal regions (including the opercular/triangular inferior frontal gyrus and pre/postcentral cortex). Also, it extended into the cerebellar lobules (e.g., lobules IV, V, and VI, Crus regions), aligning with improved, more practised coordination for tactile detection.

These group-level differences suggest that participants who spent months acquiring Braille skills by touch developed a more widespread response for detecting Braille-like dot patterns

and simple words, even in a simple 6-dot detection task. Their enhanced activity in sensorimotor, attentional, and subcortical-cerebellar circuits likely reflects the long-term neuroplastic changes induced by the Braille reading experience (Matuszewski et al., 2021).

Table 29. Main effect of group (experimental > control) in the 6-dot Detection Task.

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Superior parietal lobule	1307	14.43	-24	-65	54
L Paracentral lobule		14.41	-14	-22	76
L Postcentral gyrus		13.98	-22	-25	72
L Inferior parietal lobule		12.94	-32	-68	42
L Precentral gyrus		8.07	-22	-28	56
L Middle frontal gyrus		5.42	-24	8	54
L Supramarginal gyrus	1089	15.19	-52	-25	22
L Precentral gyrus		12.68	-62	0	32
L Postcentral gyrus		12.20	-62	-15	34
L Insula		11.77	-39	-8	12
L Triangular part of the inferior frontal gyrus		10.03	-49	25	26
L Opercular part of the inferior frontal gyrus		9.50	-49	10	19
L Inferior parietal lobule		6.68	-44	-28	36
L Putamen		6.11	-26	-2	-4
R Lobule IV, V of cerebellar hemisphere	663	9.39	8	-50	-8
R Lobule VI of vermis		7.84	4	-62	-24
R Crus II of cerebellar hemisphere		6.85	8	-78	-36
R Fusiform gyrus		6.74	31	-52	-18
R Lobule VI of cerebellar hemisphere		6.33	18	-70	-26
L Lobule IV, V of cerebellar hemisphere		5.10	-4	-52	-21
R Inferior parietal lobule	473	11.59	38	-52	54
R Superior occipital gyrus		8.82	26	-68	39
R Superior parietal lobule		8.60	28	-60	62
R Angular gyrus		8.02	28	-55	46
R Postcentral gyrus	327	16.91	66	-12	24
R Supramarginal gyrus		9.21	61	-22	32
R Rolandic operculum		7.04	51	-22	22
R Superior temporal gyrus		6.81	64	-30	19
R Precentral gyrus		6.27	64	0	29
R Calcarine cortex	86	5.98	1	-58	14
L Precuneus		5.61	-9	-42	6
R Precuneus		5.24	4	-68	26
L Posterior cingulate gyrus		5.04	-4	-48	19
R Middle occipital gyrus	73	9.23	41	-78	12
R Supplementary motor area	67	9.67	11	0	62
R Superior frontal gyrus		6.78	21	-2	54
R Postcentral gyrus	60	9.76	34	-32	42
R Opercular part of the inferior frontal gyrus	51	7.00	54	15	26
R Triangular part of the inferior frontal gyrus		5.49	46	18	22

L Inferior occipital gyrus	50	7.02	-49	-62	-14
R Insula	47	7.81	38	-8	16
L Fusiform gyrus	44	5.88	-26	-42	-21
L Lobule IV, V of cerebellar hemisphere		5.87	-22	-38	-26
R Postcentral gyrus	34	7.10	31	-38	62
R Median cingulate gyrus		6.98	14	-18	44
R Postcentral gyrus	33	7.11	48	-20	54
L Paracentral lobule	30	7.94	-4	-20	62
L Median cingulate gyrus		7.15	-12	-20	46
L Middle frontal gyrus	27	6.32	-29	38	44
L Crus I of cerebellar hemisphere	26	5.72	-14	-68	-28
R Superior frontal gyrus	25	6.25	26	38	42
R Superior temporal gyrus		6.24	61	-2	2
L Middle frontal gyrus	23	6.66	-39	58	4
L Orbital part of the middle frontal gyrus		5.32	-44	50	-6
L Thalamus	22	5.99	-9	-25	2
R Caudate	20	5.43	8	8	-4

Note. Local peaks from a contrast represent the main effect of group (experimental > control) in the 6-dot Detection Task. X, y, and z are MNI coordinates. All the presented results have been thresholded using the FWE correction ($p < 0.05$) with a cluster extent of 20 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

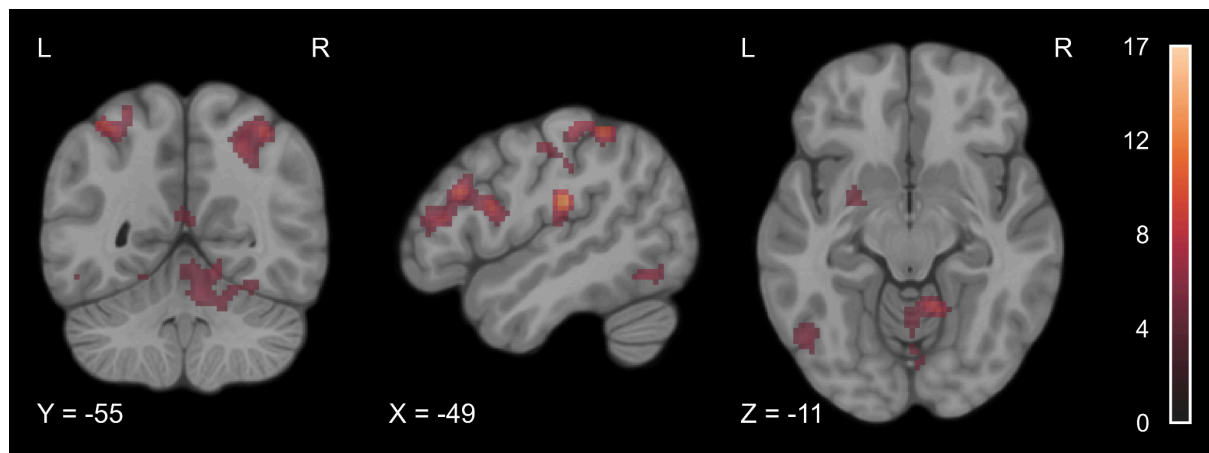


Figure 32. Statistical map of the main effect of group (experimental > control contrast) in the DD6 task. The colourmap represents the t -statistic range. We used the coordinates of the peak activity in Braille Lexical Decision tasks to visualise and facilitate comparison between images. Results were thresholded at a voxel level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.05 and a cluster extent of 20 voxels.

6.2.2.2. Main effect of group, time and group interaction

We found no significant main effect of time or time-by-group interaction.

6.3. Discussion

6.3.1. Study overview and design rationale

Sighted adults learning to read Braille by touch offers a unique window into cross-modal neuroplasticity. However, most prior studies have focused on explicit reading tasks or simple tactile pattern discrimination (Debowska et al., 2016; Y.-F. Liu et al., 2023; Matuszewski et al., 2021; Siuda-Krzywicka et al., 2016). In daily life, however, fluent reading often occurs automatically without deliberate effort (e.g. reading subtitles without intent) (Joo et al., 2021). In the visual modality, implicit reading reflects top-down engagement of the VWFA and tighter coupling with language areas during word recognition (White et al., 2023).

Whether tactile reading can become similarly automatic is not established. Given converging evidence that the core reading network, including the VWFA, can support reading independent of visual experience (Reich et al., 2011; Tian et al., 2023), we tested whether exposure to Braille words, without an explicit instruction to read, would recruit this circuitry in Braille-trained learners but not in untrained controls. To test this, we developed a 6-dot tactile detection task that all participants could perform, while a subset of trials surreptitiously contained short Braille words. This mixed-design fMRI experiment contrasted a Braille-learning group with passive controls across multiple time points to assess group differences, training-related change, and their interaction, allowing the testing of the emergence of implicit tactile reading with training. To our knowledge, prior tactile-Braille neuroimaging in sighted adults probed overt reading rather than incidental word processing, underscoring the novelty of this approach (Y.-F. Liu et al., 2023; Siuda-Krzywicka et al., 2016). We anticipated that Braille-trained individuals would show greater engagement of reading-related regions than controls during the detection task (reflecting incidental word processing), illuminating the development of automatic tactile reading.

6.3.2. Key results

Braille training did not lead to greater performance on the 6-dot detection task than passive controls. Both the learning and control groups showed improvement in accuracy over time, with a significant main effect of time. However, no reliable group difference or group and time interaction was observed. Post-hoc tests confirmed that the number of correctly detected 6-dot stimuli increased at nearly every session relative to baseline for all participants. By the end of the training period (TP₄), performance had risen from 81.3% at baseline to an average of 88.9%. Crucially, the Braille learners were no more accurate than the untrained controls, indicating that extensive Braille exposure did not improve one's ability to detect a whole

Braille cell beyond general practice effects. This lack of between-group behavioural difference likely reflects the task's simplicity - even Braille-naïve subjects can learn to feel whether all six dots are present, reaching high performance with minimal training. In other words, the detection task reached a near-ceiling level for both groups once they became familiar with it, which is beneficial for interpretation: it ensured that any brain differences were not confounded by significant performance disparities or effort differences between groups (Grinband et al., 2011; Taylor et al., 2013). The results suggest that while Braille learners acquired many new skills, their basic tactile pattern-detection ability in this task improved primarily due to repeated exposure (a training effect observed equally in the control group). Consistent with this, we did not observe far-transfer cognitive benefits of Braille learning: on unrelated tasks (e.g. an n-back working memory task and a Stroop task included in the study), both groups showed comparable practice-related changes (improving in n-back accuracy and approaching a ceiling in Stroop performance over time) with no significant group or interaction effects. Thus, any functional changes in the Braille group cannot be explained by general cognitive enhancements or greater task engagement, but are specific to the experience of learning to read by touch.

Despite exhibiting similar behaviour, the Braille-trained group displayed markedly different brain activation patterns compared to controls during the implicit reading task. A whole-brain ANOVA (6 time points x 2 groups) revealed a significant main effect of group, with Braille learners showing a higher overall level of brain activity than passive controls across a broad bilateral network. This included extensive clusters in the fronto-parietal sensorimotor regions of both hemispheres: the primary somatosensory and motor cortices (postcentral and precentral gyri), the superior and inferior parietal lobules (including the intraparietal and supramarginal regions), and the supplementary motor area. These regions are well-established substrates for tactile exploration and attention, consistent with greater finger-related sensory processing and attentional control during Braille-like scanning in learners (Klautke et al., 2023). In the left hemisphere, we also observed stronger activations in classic language/reading-associated areas for the Braille group, including the inferior frontal gyrus (opercular and triangular parts) and the VWFA. No such difference emerged in the right-hemisphere homolog of VWFA, in line with evidence that reading processes are predominantly left-lateralised (Bonandrini et al., 2024; De Rosa et al., 2024).

Braille learners likewise exhibited greater activity in subcortical and cerebellar regions. The left putamen and thalamus were more active than in controls, aligning with contemporary

accounts that corticostriatal and thalamic circuits support language and reading-related operations (Bulut & Hagoort, 2024; Copland et al., 2021). The right cerebellum (lobules IV-VI and Crus I/II) showed multiple clusters of higher activation, consistent with work implicating the right posterior cerebellum (including Crus I/II) in linguistic processing (Nakatani et al., 2023). We also observed stronger engagement of the right inferior frontal cortex and anterior insula, as well as bilateral precuneus and posterior cingulate: nodes linked to salience/control and visuo-spatial imagery/sustained attention, respectively (Yamaguchi & Jitsuishi, 2024). Altogether, this widespread pattern suggests a distributed response following months of tactile reading practice, spanning sensorimotor, attentional, language, and motor coordination systems.

Because the DD6 model yielded no main effect of time and no time-by-group interaction, the present data do not establish when learner–control differences emerged. The supported conclusion is narrower: averaged across sessions, Braille learners showed stronger DD6-related activation than passive controls. Once learners acquired a foundational grasp of the tactile code, the brain’s response to Braille-like stimuli engaging reading and sensorimotor circuits was established and did not intensify with further practice. By the first few months, the Braille group displayed an automatic tactile-reading-like response that persisted through later sessions, a pattern consistent with prior observations that recruitment often first rises early, then levels as skill consolidates (Roth & Ding, 2024). Overall, the group contrast confirms our key hypothesis: even without overt reading demands, the Braille-trained brain responds differently from the untrained brain, spontaneously activating regions ordinarily dedicated to reading. This functional reorganisation mirrors explicit Braille-reading findings in sighted learners reported in recent works (Y.-F. Liu et al., 2023; Matuszewski et al., 2021).

The presented findings are consistent with automatic reading-relevant engagement during DD6 in trained learners. However, because the task also contains tactile scanning, somatosensory attention, motor routine, and possible residual awareness of embedded words, the present data do not isolate process-pure implicit reading.

What might underlie the Braille learners’ enhanced brain responses in an ostensibly simple detection task? One likely factor is the development of reading *automaticity*. With practice, the act of decoding letters and words becomes fast and involuntary - a hallmark of skilled reading in any modality. In the visual domain, skilled readers show “automatic recruitment” of language areas when words are present, even if their attention is directed elsewhere (Joo et

al., 2021). Current results indicate that a similar transition toward automatic processing occurred for tactile reading: the trained participants could not help but engage linguistic circuits upon encountering Braille patterns, even though they were only asked to detect a physical pattern. The selective activation of left-hemisphere language regions (like Broca's area in the left inferior frontal gyrus) in Braille readers suggests that, after training, they were implicitly translating the tactile input into phonological or semantic information. In other words, their brains were treating the finger-scanned dots as meaningful words by default - consistent with the idea that reading by touch, like sight-reading, can become an automatic, stimulus-driven response (Price & Devlin, 2011). This automaticity is closely tied to the concept of *predictive coding* (Zhao et al., 2019). According to interactive models of reading, the visual word form area and connected language regions actively generate top-down predictions about incoming stimuli. Once the brain has learned an orthography, simply feeling a familiar letter sequence may trigger expectations of the entire word, engaging the reading network even without conscious effort to read. We interpret that when the fingertip encountered Braille letters, higher-level areas (frontal and temporal language regions) were automatically predicting and "filling in" the linguistic content - thereby explaining the extra activation in those areas compared to controls. This is supported by the co-activation of motor and somatosensory areas: Braille reading is an active sensing process, and the brain likely uses an internal forward model to predict the tactile consequences of hand movements. The cerebellum's involvement provides a compelling hint of such mechanisms. The cerebellum is increasingly recognised not just for motor coordination but also for generating predictive signals in cognitive and language domains (Lesage et al., 2012). Disrupting right cerebellar function has been shown to impair people's ability to anticipate upcoming words in spoken sentences, highlighting that the cerebellum aids linguistic prediction. Here, greater cerebellar activation in Braille readers may reflect the use of an internal model to predict the sequence of dots one expects to feel next, based on learned letter patterns and the ongoing finger motion. By predicting forthcoming tactile inputs, the cerebellum (and its connected cortical networks) could facilitate the smoother and faster identification of Braille characters - essentially automating the reading process at a sensorimotor level. In parallel, the engagement of the basal ganglia (e.g., putamen) in Braille learners suggests the *proceduralization* of the task. The basal ganglia play a crucial role in habit learning and the automatising of skills, particularly when a sequence of actions or sensorimotor associations is practised repeatedly (Ashby et al., 2010). The Braille-reading group had spent months

drilling the movements and perceptual cues for dot patterns, effectively converting what was initially a slow, cognitive endeavour into a more reflexive motor-cognitive routine. The elevated activity in the putamen and thalamus suggests that these subcortical circuits supported learners' performance on the tactile reading task, consistent with a partially proceduralized skill: they were likely chunking Braille patterns and finger movements into learned units (Yin & Knowlton, 2006). Likewise, the supplementary motor area and premotor involvement could indicate the encoding of Braille reading as a learned motor sequence (scanning and recognising patterns), now executed with less conscious oversight (Dayan & Cohen, 2011; Hardwick et al., 2013). Together, these points paint a picture of how the brain adapts to incorporate a new sensory reading modality: the process becomes *automatic* (engaging reading and language areas without intent), driven by *predictive* mechanisms (top-down expectations and forward models to anticipate sensory input), and increasingly *procedural* (relying on habitual motor-sensory loops involving cerebellum and basal ganglia) (Sokolov et al., 2017). The activation patterns we observed align with systems known to support automatic and predictive processing. Future studies could directly test these mechanisms, for example, by perturbing the cerebellum or frontal areas with brain stimulation to see whether this disrupts implicit Braille reading, or by examining whether indicators of prediction (such as suppressed responses to expected vs unexpected Braille inputs) are present in trained readers. At this stage, our findings are consistent with the notion that months of Braille training enable the brain to automatically and optimally interpret tactile words by harnessing the same networks used in conventional reading, augmented by sensorimotor predictive loops that streamline the translation of touch into language.

7. Braille processing in sighted learners and blind readers

To what extent do sighted individuals trained in tactile reading activate networks similar to those of congenitally blind, proficient Braille readers? What are the differences in brain activation patterns between sighted and congenitally blind individuals during tactile reading? How does the mode of tactile stimulus presentation affect the differences in activation between sighted and congenitally blind individuals? How do explicit versus implicit processing of Braille characters differ in activation between sighted and congenitally blind individuals?

Previous research highlighted how sensory deprivation prompts extensive cortical reorganisation in blind individuals. Plasticity can be observed in the visual cortex following auditory stimulation (Ortiz-Terán et al., 2016) and tactile stimulation (Burton et al., 2004), including both early sensory regions (Sadato et al., 1996) and higher-order visual areas (Büchel, Price, Frackowiak, et al., 1998), as well as the reading network (Reich et al., 2011). Furthermore, such plasticity can persist even after the lost sense is restored, highlighting its role in maintaining functional activity (Mowad et al., 2020). At the same time, Braille training engages basic motor and sensory regions and brain areas associated with higher-order cognitive functions in sighted people, providing a comprehensive model to study cross-modal plasticity (Matuszewski et al., 2021).

7.1. Aims, research questions, and predictions

This cross-sectional study was designed to compare tactile Braille processing in sighted learners at the end of training with that in congenitally blind, proficient Braille readers. The aim was to identify which aspects of explicit and implicit Braille processing are shared across groups and which differ as a function of sensory experience and reading experience.

It addressed the following research questions:

1. Which regions are shared between sighted learners and congenitally blind Braille readers during tactile Braille lexical decision?
2. Which regions differ between groups during tactile Braille lexical decision?
3. Do similar shared-versus-group-specific patterns appear during the 6-dot detection task?
4. Do blind readers show stronger occipital and occipitotemporal recruitment, whereas sighted learners show stronger frontoparietal and sensorimotor recruitment?

5. How should between-group differences be interpreted in relation to sensory experience, expertise, and task demands rather than any single factor alone?

The main predictions were as follows. Both groups were expected to recruit a shared higher-level tactile reading network during explicit Braille reading, especially in the inferior frontal and ventral occipitotemporal regions. Blind readers were expected to show stronger recruitment in the occipital and occipitotemporal regions, consistent with long-term reorganisation associated with congenital blindness. In contrast, sighted learners were expected to show greater recruitment of frontoparietal, sensorimotor, and control-related regions consistent with more effortful tactile decoding. For the 6-dot detection task, overlap was expected in dorsal sensorimotor-attentional systems, with any blind-greater-than-sighted effects again concentrated in occipital territories. These comparisons were intended to characterise shared and divergent implementations of tactile reading, not to conclusively isolate deprivation effects from expertise or training stage.

7.2. Results

7.2.1. Tactile Braille Lexical Decision Task

7.2.1.1. Conjunction of activity

A cross-group conjunction (sighted vs blind) indicated a common set of regions involved in processing Braille words by touch (see **Table 30** and **Figure 33**). In the left hemisphere, a cluster centred on the inferior temporal gyrus indicates involvement of the VWFA. The precentral gyrus and the opercular/triangular/orbital parts of the inferior frontal gyrus were also activated, suggesting a motor-linguistic core that both sighted and blind individuals recruit when tactually decoding Braille. Subcortically, the left thalamus emerged, highlighting its role as a critical relay for somatosensory signals.

Mirroring these findings on the right side, the inferior frontal gyrus (opercular, triangular, and orbital divisions) and the precentral gyrus showed common activation across groups, implying bilateral frontal engagement in controlling or planning the reading-by-touch process. Additional involvement of the supplementary motor area bilaterally corroborates the notion of a shared motor-executive network across blind and sighted readers. Subcortical nodes, such as the right thalamus, underscore symmetrical sensory integration, while the calcarine cortex on the left signals possible cross-modal or attention-related reallocation of “visual” areas for tactile reading.

Finally, extensive cerebellar peaks (including lobule VI, Crus I/II, and vermal regions) appeared for blind and sighted readers, consistent with the cerebellum’s known role in fine

motor control and error correction while scanning Braille with the fingertips. These conjunction results reveal a broad, bilateral sensorimotor-linguistic network that underpins tactile Braille reading in both sighted and blind individuals, indicating a fundamental cross-modal architecture for Braille-specific decoding and higher-level language processing (Burton et al., 2002).

Table 30. The conjunction of activity in sighted and blind in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior temporal gyrus	1879	7.60	-49	-50	-11
L Lobule VI of cerebellar hemisphere		6.96	-24	-70	-18
R Lobule VI of cerebellar hemisphere		5.58	34	-65	-21
R Crus II of cerebellar hemisphere		5.48	6	-82	-34
L Crus I of cerebellar hemisphere		5.13	-39	-68	-24
L Lobule VIII of vermis		4.93	-2	-60	-26
L Crus II of cerebellar hemisphere		4.77	-6	-80	-31
R Lobule VIIB of cerebellar hemisphere		4.37	18	-80	-48
L Lobule IV, V of cerebellar hemisphere		3.81	-12	-52	-24
L Precentral gyrus	1689	6.53	-46	2	42
L Orbital part of the inferior frontal gyrus		6.02	-44	22	-4
L Opercular part of the inferior frontal gyrus		5.94	-52	12	26
L Insula		5.38	-34	20	-4
L Triangular part of the inferior frontal gyrus		5.38	-44	30	2
L Postcentral gyrus		3.87	-49	-12	46
R Triangular part of the inferior frontal gyrus	796	5.82	48	30	6
R Orbital part of the inferior frontal gyrus		5.60	41	28	-4
R Opercular part of the inferior frontal gyrus		5.48	38	8	24
R Precentral gyrus		5.11	54	8	42
R Insula		4.33	38	28	6
R Middle frontal gyrus		3.67	48	-2	54
R Supplementary motor area	419	5.08	6	8	64
L Supplementary motor area		4.83	-9	12	52
R Medial part of the superior frontal gyrus		4.50	4	30	49
L Thalamus	205	5.76	-12	-18	2
L Calcarine cortex	123	4.65	-9	-82	6
R Thalamus	97	4.16	11	-12	6

Note. Local peaks from a contrast represent a one-sample t-test - the conjunction of activity for both sighted and blind groups for experimental > control contrasts. All the presented results have been thresholded using the cluster-level FWE correction of 97 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

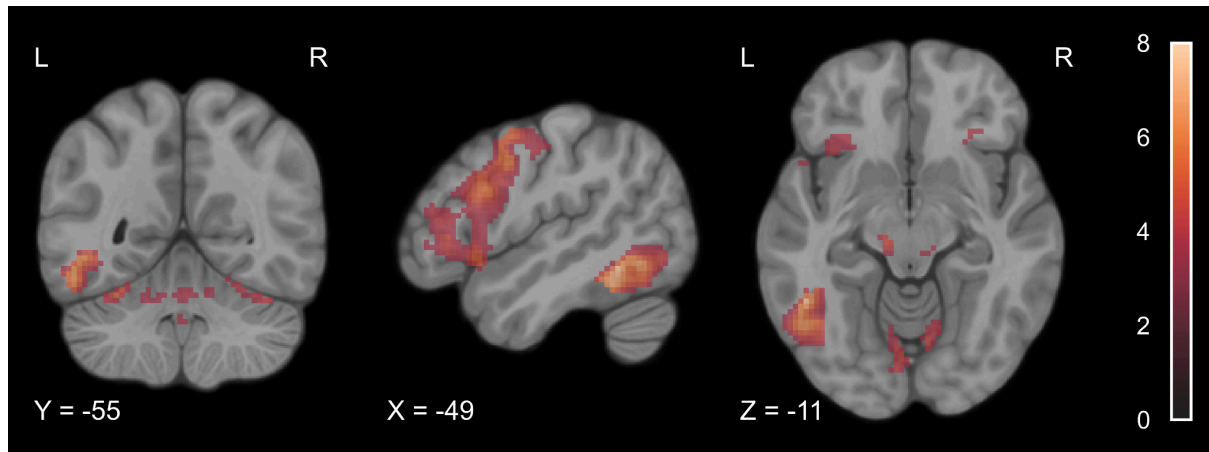


Figure 33. Statistical map of the conjunction of activity of sighted and blind groups for experimental > control contrast in the tactile Braille Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparisons correction with a p -value of 0.001 and a cluster extent of 97 voxels.

7.2.1.2. Sighted > blind

When comparing sighted to congenitally blind Braille readers, sighted participants showed greater activation in a broad bilateral network of parietal-frontal-subcortical regions for tactile Braille words (see **Table 31** and **Figure 34**). In both hemispheres, strong sensorimotor involvement encompassed the precentral and postcentral gyri, the inferior and superior parietal lobules, and the supplementary motor area, highlighting a possibly more effortful or distinctive motor-somatosensory strategy that sighted individuals use when reading by touch. Additional peaks in the anterior/median cingulate and precuneus also emerged, suggesting heightened attentional, executive, or default-mode adjustments in sighted readers.

Subcortically, both thalamus (left and right) and basal ganglia structures (e.g., putamen, caudate) were more active in the sighted group, consistent with increased reliance on sensory relay and motor habit circuits. Insular involvement indicates greater salience or interoceptive processing in the sighted cohort for tactile decoding. Moreover, cerebellar clusters (e.g., right lobule VI, Crus I) supported ongoing fine motor coordination during Braille scanning.

Overall, these findings suggest that sighted Braille readers rely more on a bilateral parietal-frontal motor-somatosensory network and subcortical relays when reading by touch, potentially compensating for their less-practised tactile skills relative to blind individuals (who have adapted to a purely somatosensory approach since birth).

Table 31. The comparison of sighted > blind in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Precentral gyrus	1321	6.63	-39	-15	66
L Inferior parietal lobule		6.50	-49	-32	44
L Superior frontal gyrus		6.40	-26	-8	59
L Postcentral gyrus		5.39	-59	-18	32
R Postcentral gyrus	683	6.42	38	-32	44
R Inferior parietal lobule		5.44	38	-45	52
R Supramarginal gyrus		5.08	58	-18	26
R Superior parietal lobule		3.80	36	-52	56
L Supplementary motor area	648	6.42	-6	2	56
R Supplementary motor area		5.90	6	20	46
R Anterior cingulate gyrus		5.41	8	20	29
R Median cingulate gyrus		4.33	14	12	36
R Precuneus	441	6.51	16	-65	46
R Superior parietal lobule		5.43	26	-65	54
L Putamen	431	7.03	-22	8	4
L Insula		6.17	-29	28	6
L Caudate		4.98	-16	-2	19
R Thalamus	412	5.38	4	-12	-1
L Thalamus		5.04	-14	-12	9
R Putamen		4.80	24	8	6
R Caudate		4.65	14	8	12
R Superior frontal gyrus	323	6.66	24	-2	54
R Lobule VI of cerebellar hemisphere	205	5.37	26	-55	-26
R Crus I of cerebellar hemisphere		3.93	31	-60	-34
R Insula	133	4.43	34	20	9
L Superior parietal lobule	124	5.63	-16	-65	52
L Middle occipital gyrus		5.01	-29	-70	32
L Precentral gyrus	116	4.78	-54	5	22
L Opercular part of the inferior frontal gyrus		3.39	-49	10	-1
R Middle frontal gyrus	106	4.91	36	45	29

Note. Local peaks from a contrast represent a two-sample t-test comparison of sighted > blind for experimental > control contrasts. All the presented results have been thresholded using the cluster-level FWE correction of 106 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

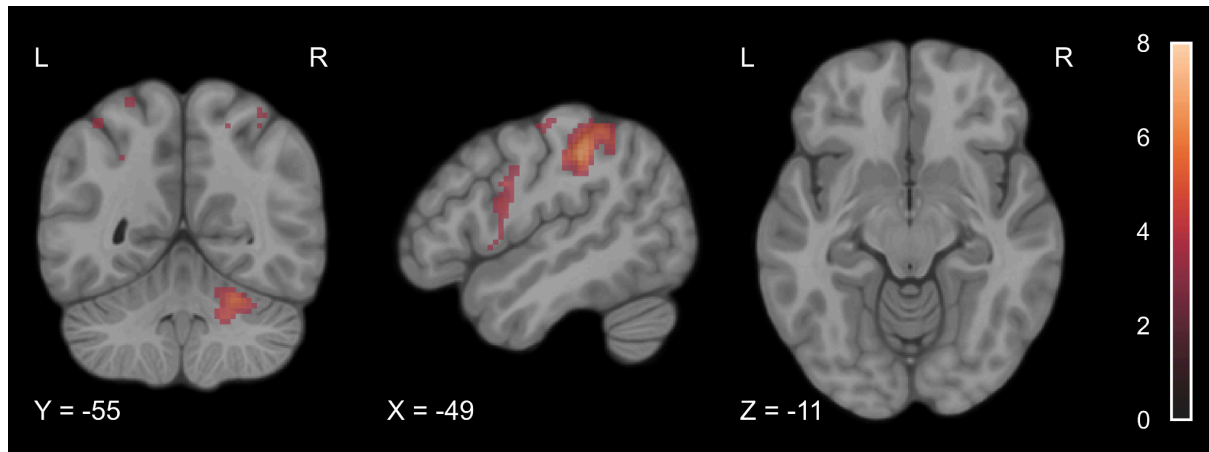


Figure 34. Statistical map of the sighted > blind groups comparison for experimental > control contrast in the tactile Braille Lexical Decision Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparison correction with a p -value of 0.001 and a cluster extent of 106 voxels.

7.2.1.3. Blind > sighted

In contrast to sighted participants, blind Braille readers displayed greater activity across occipitotemporal and limbic structures when reading Braille by touch (see **Table 32** and **Figure 35**). Bilateral middle/inferior occipital gyri, fusiform gyri, middle/inferior temporal gyri, and the angular gyrus emerged prominently, suggesting enhanced cross-modal recruitment of “visual” areas for tactile language processing. Subcortical regions, including the left and right hippocampi and the right amygdala, were also significantly more active, which may indicate memory-related or emotion-salience components associated with Braille reading in blind individuals.

Additionally, the precuneus and median cingulate were more engaged in the blind group, reflecting visuospatial imagery or default-mode network adaptations for tactile decoding. These findings imply that congenitally blind Braille readers leverage broader occipitotemporal and limbic networks for reading by touch, likely reflecting long-standing cross-modal plasticity and reliance on nonvisual memory and semantic-emotional contexts in the absence of visual experience.

Table 32. The comparison of blind > sighted in the tactile Braille Lexical Decision Task (experimental > control).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
R Middle temporal gyrus	767	5.29	51	-65	6
R Fusiform gyrus		5.22	38	-55	-18
R Middle occipital gyrus		5.01	48	-80	2
R Inferior occipital gyrus		4.73	34	-78	-11
R Inferior temporal gyrus		4.31	46	-72	-8
L Middle occipital gyrus	720	5.94	-39	-80	-1
L Fusiform gyrus		5.85	-29	-72	-14
L Middle temporal gyrus		4.17	-54	-68	12
L Angular gyrus	526	6.19	-39	-58	26
L Middle temporal gyrus		6.09	-46	-52	19
L Supramarginal gyrus		5.39	-54	-55	26
L Hippocampus		6.06	-16	-8	-18
L Inferior temporal gyrus	327	4.44	-42	-25	-18
L Parahippocampal gyrus		4.17	-29	-28	-21
R Cuneus	305	6.11	4	-95	16
L Middle occipital gyrus		4.58	-19	-95	14
L Superior occipital gyrus		4.55	-19	-90	26
R Hippocampus	257	6.02	21	-8	-14
R Amygdala		5.53	31	2	-28
L Precuneus	141	4.70	-9	-50	44
L Median cingulate gyrus		4.54	-12	-45	36

Note. Local peaks from a contrast represent a two-sample t-test comparison of blind > sighted for experimental > control contrasts. All the presented results have been thresholded using the cluster-level FWE correction of 141 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

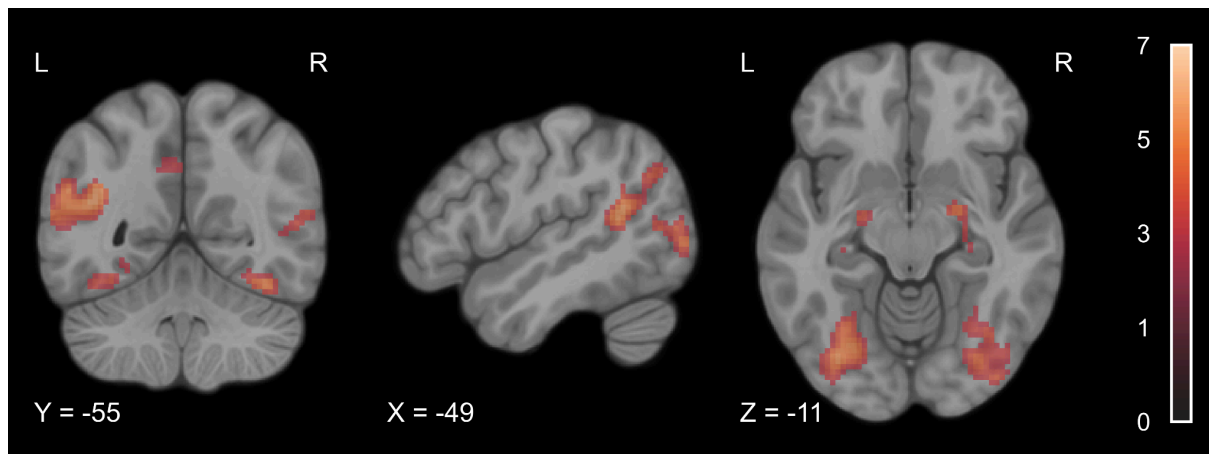


Figure 35. Statistical map of the blind > sighted groups comparison for experimental > control contrast in the tactile Braille Lexical Decision Task. The colour map represents the *t*-statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparisons correction with a p-value of 0.001 and a cluster extent of 141 voxels.

7.2.2. 6-dots Detection task

7.2.2.1. Conjunction of activity

A large bilateral network emerged as consistently active during the 6-dot detection task in both sighted and blind Braille readers (see **Table 33** and **Figure 36**). Widespread sensorimotor regions spanning the precentral and postcentral gyri, supplementary motor area, and inferior and superior parietal lobules were engaged, indicating that both groups recruited similar frontoparietal resources for detecting and identifying Braille-like dot patterns. Subcortical areas, particularly the basal ganglia (putamen, caudate) and the insula, also contributed to shared motor coordination, salience, and feedback mechanisms in tactile discrimination.

Moreover, extensive cerebellar involvement (e.g., lobules VI and VIII, Crus I/II, and vermal regions) was present in both groups, highlighting motor control and spatial timing processes that are fundamental to the exploration of raised-dot stimuli. Occipital clusters (calcarine, cuneus, middle occipital gyrus) were also active. This suggests that participants, regardless of sight status, employed cross-modal or visual-related attentional resources, possibly for spatial mapping of tactile inputs. Additional frontal peaks (in the left and right middle frontal gyrus and triangular inferior frontal gyrus) underscored higher-level executive or attentional engagement in discriminating 6-dot patterns and implicit reading.

Altogether, these conjunction findings reveal a bilateral sensorimotor, subcortical, and cerebellar network that underpins dot-pattern detection and implicit reading in both blind and sighted individuals. This network reflects fundamental processes of touch-based exploration, motor planning, and spatial attention shared across sensory backgrounds.

Table 33. The conjunction of activity in sighted and blind in the 6-dot Detection task (experimental).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Precentral gyrus	14014	13.09	-39	-15	62
R Postcentral gyrus		12.97	41	-30	44
L Postcentral gyrus		12.29	-59	-18	32
L Supplementary motor area		12.12	-6	2	54
L Inferior parietal lobule		11.94	-52	-32	49
L Insula		11.90	-32	18	4
R Opercular part of the inferior frontal gyrus		11.79	56	8	22
L Rolandic operculum		11.75	-42	-5	14
R Putamen		11.73	21	8	6
R Insula		11.57	38	0	16
R Superior frontal gyrus		11.27	21	-2	56
R Inferior parietal lobule		11.20	38	-45	54
L Caudate		9.96	-14	10	6
R Supramarginal gyrus		9.95	58	-15	26
L Putamen		9.88	-24	-2	4
L Superior parietal lobule		9.33	-34	-55	59
R Lobule VI of cerebellar hemisphere	6637	11.98	21	-55	-24
L Lobule VIII of cerebellar hemisphere		10.73	-26	-65	-58
R Lobule VIII of cerebellar hemisphere		10.08	18	-68	-46
L Lobule VIIB of cerebellar hemisphere		9.55	-14	-75	-48
R Lobule IV, V of vermis		9.43	6	-62	-14
L Lobule VI of cerebellar hemisphere		9.21	-24	-70	-21
L Crus I of cerebellar hemisphere		8.62	-34	-55	-34
R Crus I of cerebellar hemisphere		8.45	44	-60	-28
R Lobule VIII of vermis		7.42	1	-75	-36
L Calcarine cortex		6.63	-6	-90	6
L Cuneus		6.20	-2	-80	22
L Lobule IV, V of cerebellar hemisphere		6.19	-16	-52	-26
R Calcarine cortex		5.99	8	-88	4
R Cuneus		5.33	8	-92	19
L Lobule IX of cerebellar hemisphere		4.59	-14	-52	-58
L Middle occipital gyrus		3.98	-22	-92	16
R Middle frontal gyrus	415	6.08	38	45	26
L Middle frontal gyrus	231	4.79	-36	48	22
L Triangular part of the inferior frontal gyrus		4.44	-32	30	26

Note. Local peaks from a contrast represent a one-sample t-test - the conjunction of activity for both sighted and blind groups for the experimental contrast. All the presented results have been thresholded using the cluster-level FWE correction of 231 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

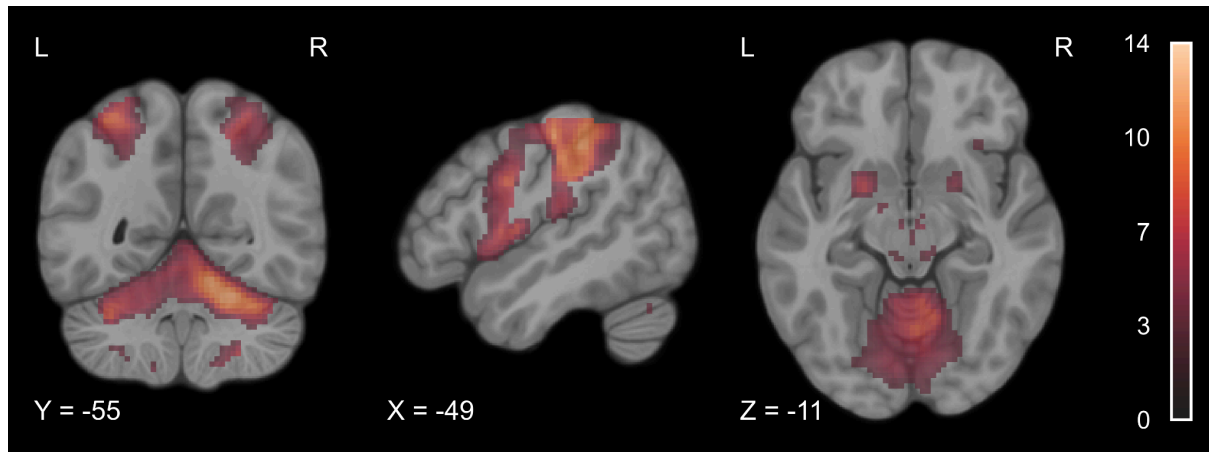


Figure 36. Statistical map of the conjunction of activity of sighted and blind groups for experimental contrast in the 6-dot Detection Task. The colour map represents the t -statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparisons correction with a p -value of 0.001 and a cluster extent of 231 voxels.

7.2.2.2. Sighted > blind

A large cluster in the occipital and parietal cortex emerged as more active for sighted Braille readers than blind readers (see **Table 34** and **Figure 37**). The cuneus and calcarine cortex in each hemisphere, and the lingual gyrus and precuneus, exhibited greater involvement in sighted individuals, suggesting that they may recruit visual-association or imagery-based processes even in a tactile-oriented task. Additional peaks in the superior/middle temporal gyri suggest that auditory or language-related regions are more strongly engaged in sighted readers, possibly reflecting cross-modal or phonological integration in an implicit reading context.

The precentral gyrus also showed greater activation in the left hemisphere, suggesting a motor planning or sensorimotor dimension that might differ between groups. Overall, these findings imply that during tactile dot detection, sighted participants engage more visuospatial cortical networks and certain temporal-linguistic areas than blind participants do, potentially reflecting a reliance on covert visual strategies or residual orthographic representations when confronted with Braille-like stimuli.

Table 34. The comparison of sighted > blind in the 6-dot Detection task (experimental).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
R Cuneus	2648	7.56	8	-70	24
L Precuneus		5.57	-22	-52	4
R Superior occipital gyrus		5.55	21	-68	32
R Lingual gyrus		5.50	11	-58	9
L Calcarine cortex		5.30	-14	-58	9
R Precuneus		5.09	24	-50	2
L Lingual gyrus		4.87	-12	-80	-8
R Calcarine cortex		4.67	26	-60	6
L Parahippocampal gyrus		4.53	-16	-38	-11
R Lobule VI of cerebellar hemisphere		4.43	21	-55	-24
R Superior temporal gyrus	712	7.12	68	-20	4
R Middle temporal gyrus		5.05	48	-50	16
L Middle temporal gyrus	705	5.58	-62	-18	-1
L Superior temporal gyrus		4.60	-54	-28	4
L Precentral gyrus	262	5.18	-39	-20	54
L Middle occipital gyrus	188	5.48	-36	-72	32
L Middle temporal gyrus		5.13	-44	-65	22

Note. Local peaks from a contrast represent a two-sample t-test comparison of sighted > blind for the experimental contrast. All the presented results have been thresholded using the cluster-level FWE correction of 188 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

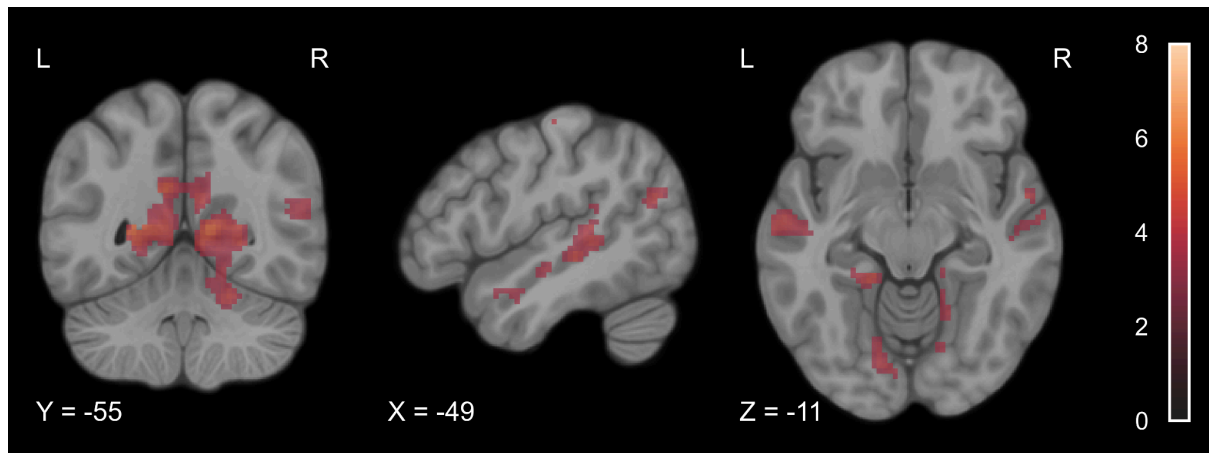


Figure 37. Statistical map of the sighted > blind groups comparison for experimental contrast in the 6-dot Detection Task. The colour map represents the *t*-statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparisons correction with a p-value of 0.001 and a cluster extent of 188 voxels.

7.2.2.3. Blind > sighted

Compared to sighted readers, blind Braille readers showed heightened activation in bilateral occipital-temporal regions during the DD6 task (see **Table 35** and **Figure 38**). On the left, a cluster centred on the inferior occipital gyrus extended into the cerebellar Crus I, whereas on

the right, the middle and inferior occipital gyri and the inferior temporal gyrus were more active. These findings underscore cross-modal plasticity in blind individuals, who may exploit visual “association” areas for tactile tasks, particularly since the 6-dot detection paradigm contains elements of implicit Braille-like reading.

The involvement of cerebellar lobules (Crus I on the left side) aligns with sensorimotor or timing coordination for exploratory touch, potentially reflecting highly adapted scanning methods in the blind. Overall, these occipital-temporal and cerebellar peaks unique to blind participants highlight more specialised cross-modal recruitment for dot detection, allowing them to rely on reallocated “visual” networks for non-visual reading-like tasks.

Table 35. The comparison of blind > sighted in the 6-dot Detection task (experimental).

<i>Region Label</i>	<i>Cluster extent</i>	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>
L Inferior occipital gyrus	420	4.90	-46	-75	-4
L Crus I of cerebellar hemisphere		4.23	-36	-80	-21
R Middle occipital gyrus	327	7.38	28	-98	2
R Inferior occipital gyrus		6.44	36	-90	-8
R Inferior temporal gyrus	122	6.46	48	-65	-11

Note. Local peaks from a contrast represent a two-sample t-test comparison of blind > sighted for experimental contrast. All the presented results have been thresholded using the cluster-level FWE correction of 122 voxels. X, Y and Z are MNI coordinates. Labels based on the AAL atlas.

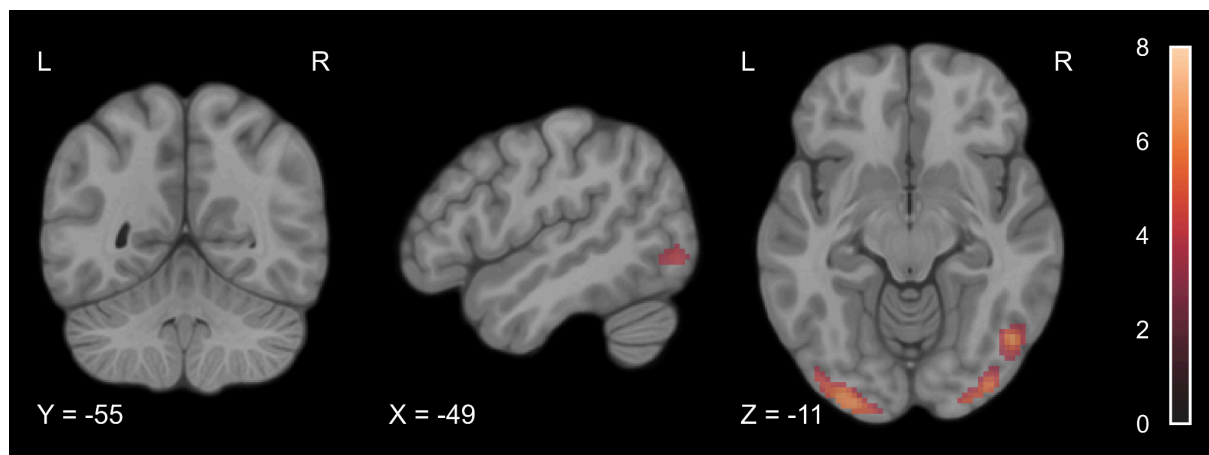


Figure 38. Statistical map of the blind > sighted groups comparison for experimental contrast in the 6-dot Detection Task. The colour map represents the *t*-statistic range. The map coordinates represent peak activity in the visual word form area in all Braille Lexical Decision Tasks. Results were thresholded at a cluster level with a Family-Wise Error (FWE) comparison correction with a p-value of 0.001 and a cluster extent of 122 voxels.

7.3. Discussion

7.3.1. Study overview and design rationale

This study aimed to identify which brain networks are shared versus group-specific when adults process Braille characters explicitly (lexical decision task, LDT) and implicitly (pattern detection task, "6-dot" detection), by comparing congenitally blind, proficient Braille readers to sighted adults who had completed intensive Braille training. This complements, without repeating, the prior longitudinal analysis (which focused on training dynamics in sighted learners) by allowing comparison of tactile-reading network implementations under different sensory experiences and experience levels. This direct juxtaposition of lifelong tactile literacy under visual deprivation with end-of-training tactile performance in sighted controls is novel - few studies have taken this approach. It addresses a gap in understanding of how early sensory loss affects the networks supporting a learned skill (Braille reading) without fully disentangling the effects of deprivation, expertise, age, sex, or training stage (Abboud & Cohen, 2019; Dziegiel-Fivet et al., 2021; Kim et al., 2017).

7.3.2. Key results

Despite vastly different sensory development, blind and sighted Braille readers share a core network for explicit reading decisions (Reich et al., 2011). The common inferior frontal gyrus-premotor-thalamic-cerebellar scaffold we observed aligns with models of reading that involve integrating bottom-up sensory evidence (in this case, tactile inputs) with top-down linguistic predictions (letter-to-phonology/semantics), regardless of the input modality (Price & Devlin, 2011). In other words, both groups appear to recruit a "reading-by-touch" circuitry that combines somatosensory processing with higher-order language control. At the same time, the extra occipito-temporal engagement in blind readers fits with evidence that ventral "visual" regions in the blind brain become tuned to language processing via cross-modal plasticity - not via visual input, but via connectivity with frontal and temporal language areas (Bedny et al., 2011; Kanjlia et al., 2021). Blind participants' occipital activation during Braille LDT likely reflects co-opting of the VWFA for reading via such top-down connectivity. This is consistent with connectivity studies showing that the blind occipital cortex is functionally coupled with fronto-temporal language networks (rather than visual networks) during linguistic tasks (Bedny et al., 2011). Thus, the blind-greater-than-sighted occipitotemporal recruitment is consistent with deprivation-related reorganisation, but the present cross-sectional design does not permit a deprivation-only inference.

The implicit-task results echo the central cross-sectional theme: both groups share a broad dorsal sensorimotor-attentional infrastructure, but group differences manifest in occipital-temporal regions (and to some extent, the cerebellum). In blind individuals, even a rudimentary tactile pattern engages the occipital cortex more than it does in sighted individuals. This suggests that the blind brain's reorganisation for touch extends beyond formal reading into simpler tactile perception tasks. Notably, the dorsal stream (parietal cortex) was active in both groups for pattern detection, aligning with its supramodal role in spatial processing and attention. The occipital recruitment in blindness for the implicit task, while weaker than in the explicit task, is still present - blind readers "bring online" visual areas during tactile perception that sighted readers do not need to use. This replicates the cross-modal plasticity observed in the explicit Braille reading task and is consistent with prior literature. For example, a recent study demonstrated that Braille reading by touch strongly engages the posterior parietal cortex in blind individuals, supporting the notion that dorsal attention networks are involved in the spatial coding of orthographic patterns in the absence of vision (Y.-F. Liu et al., 2023). Our findings extend this: blind individuals exhibit greater occipital activation than sighted individuals during an implicit tactile task, consistent with reports of visual cortex involvement across various tasks in the blind (Dzięciel-Fivet et al., 2021; Striem-Amit et al., 2012). In contrast, sighted Braille learners, even when not required to identify letters explicitly, seem to tap into visuospatial mental resources (e.g., occipital and parahippocampal regions), possibly reflecting covert visualisation or template-matching strategies. In summary, the cross-sectional comparison reveals a pattern: common networks where task demands overlap, and divergences chiefly in how the occipital-temporal system is recruited (high engagement in the blind, comparatively low in the sighted) and how the cerebellar and attentional control systems may be differentially engaged.

The blind > sighted enhancement of occipito-temporal activation (in Braille LDT, and to a lesser degree in DD6) aligns with extensive evidence that in congenital blindness, the VWFA becomes responsive to language and reading irrespective of input modality. Studies have shown that tasks such as Braille reading or listening to spoken letters activate the VWFA in individuals who are blind (Reich et al., 2011; Striem-Amit et al., 2012), supporting the notion of a metamodal reading network that is independent of visual experience. Current results reinforce that idea by showing that blind Braille readers activate this region more strongly than sighted Braille readers under equivalent task conditions.

At the same time, the presence of the left inferior frontal gyrus and thalamocerebellar co-activation in both groups aligns with interactive, predictive coding accounts of reading. In these accounts, higher-order language regions (such as the left inferior frontal gyrus) send top-down constraints to orthographic processing regions to facilitate recognition (Price & Devlin, 2011). Our data show that the inferior frontal gyrus co-activates with VWFA, suggesting that such feedback mechanisms are at play in tactile reading. The co-activation of the thalamus and cerebellum points to their roles in a distributed network that supports Braille reading. This dovetails with recent frameworks that emphasise reading (and other cognitive skills) as distributed over cortico-subcortical loops. For example, the cerebellum is increasingly recognised as a "predictive engine" in language tasks, helping to time the sequencing of inputs and perhaps to detect deviation from expected patterns (Gagl et al., 2020; Gatti et al., 2021). Likewise, the basal ganglia and thalamus are thought to support the automatisisation of sequences and the gating of attention (Alm, 2021; Silveri, 2021) - functions clearly relevant for developing fluent Braille reading. The DD6 task's shared activation of thalamus (sensory relay), striatum, and cerebellum fits with this view, as these subcortical structures likely contribute to the rhythmic scanning and expectation aspects of tactile pattern processing.

The pattern of subcortical and cerebellar involvement we observed converges with broader views of cognition that include these structures. The thalamus, basal ganglia, and cerebellum form loops with the cortex that are known to underlie sensorimotor skills and cognitive sequencing. In language and reading, these loops are believed to assist in automatisisation (e.g., the basal ganglia "chunking" a learned sequence of letters or movements into a fluid routine) and error correction/prediction (the cerebellum comparing expected vs actual sensory feedback and helping adjust timing) (Alm, 2021; Gatti et al., 2021; Silveri, 2021). Our DD6 conjunction, which showed common thalamic, putaminal, and cerebellar activation across groups, fits with this view: both blind and sighted likely rely on cortico-subcortical loops to parse the rapid sequence of dot stimuli and maintain attention to the pattern. The cerebellar Crus I/II activation across both tasks (especially right Crus I/II for LDT and left Crus I for blind > sighted in DD6) is particularly interesting in light of contemporary models positing the cerebellum's role in language prediction and timing (Jobson et al., 2024; LeBel & D'Mello, 2023). Our data add evidence from a tactile modality that the cerebellum consistently participates when timing and sequencing demands are high (Braille reading by touch certainly has these demands). Our observation of the contributions of the parietal and

dorsal attention systems aligns with the established roles of the parietal lobe in Braille reading. The posterior parietal cortex (especially the supramarginal gyrus and superior parietal lobule) has been implicated in processing Braille orthography, including coding the number of characters and the spatial configuration of Braille dots (e.g., Braille cell patterns and word length) (Y.-F. Liu et al., 2023). Blind readers often show heightened parietal activation, possibly reflecting the conversion of visual-spatial working memory systems to handle tactile spatial information. In our data, the engagement of both groups in the superior parietal lobule/precuneus for Braille tasks suggests that spatial attention and sequential processing are necessary for perceiving dot patterns. At the same time, the blind > sighted difference in the left angular gyrus during LDT might relate to multimodal integration or semantic processing in the blind (since the angular gyrus is a cross-modal integration area often involved in language). The fact that sighted > blind differences in parietal areas were modest (a slight advantage for sighted in right dorsal superior parietal lobule in LDT, whereas blind readers had a left supramarginal gyrus advantage) indicates that both groups heavily rely on parietal cortex - reinforcing that this is a truly supramodal aspect of Braille processing.

Finally, the consistent cerebellar involvement we found (notably Crus I, Crus II, and lobule VI across various contrasts) is worth noting in light of emerging cerebellar theories (Guell et al., 2018). Once thought to be purely motor, the cerebellum is now recognised as contributing to language and cognition by predicting sensory outcomes and facilitating the chunking of sequences (e.g., syllables or letters) for fluent processing. Our results, showing Crus I/II activity in both blind and sighted Braille reading, align with this view. Moreover, the left Crus I activation, which was stronger in blind readers (in the DD6 task), might suggest that blind individuals, through extensive tactile experience, have developed remarkably fine-tuned cerebellar predictions for hand movements during Braille pattern exploration. This is speculative, but it fits with models in which the cerebellum helps optimise movements based on expected tactile feedback - something expert blind Braille readers would have in abundance. In support of this idea, contemporary research positions the cerebellum firmly "at the table" in language processing networks (LeBel & D'Mello, 2023). It demonstrates structural connectivity linking the cerebellum to cerebral language areas (Jobson et al., 2024). Thus, our finding of cerebellar engagement provides a functional substrate for these theoretical roles in the context of tactile language.

In summary, the cross-sectional comparisons were designed and analysed to minimise bias. The groups differ in some demographic factors (age, sex, training level). However, these were accounted for conceptually and do not plausibly explain the specific pattern of results we found (notably the selective occipital-temporal reorganisation seen in blind readers). Our interpretations remain valid under the scrutiny of these potential confounds. Where uncertainties exist (e.g., lack of direct behavioural comparisons), we have either acknowledged them or used external evidence to argue that they are not driving the effects (as with the difficulty argument for occipital activation). The core message - that congenital blindness leads to the incorporation of the occipital cortex into the Braille reading network, atop a shared tactile-language scaffold - is strongly supported, even when considering these limitations.

This cross-sectional study opens several avenues for further investigation, both to verify causal relationships in the network and to explore structural underpinnings:

A compelling next step is to use noninvasive brain stimulation to test the causal role of feedback from frontal language areas to the occipital cortex in blind Braille reading. For example, applying repetitive TMS to the left inferior frontal gyrus (as opposed to a control site, such as the vertex or occipital pole) in blind Braille readers during the LDT could reveal whether disrupting frontal feedback disproportionately affects occipital activation and Braille reading performance in the blind. If blind readers rely on top-down input to the occipital cortex, perturbing the left inferior frontal gyrus should reduce occipital responses and perhaps impair decision accuracy more in the blind group than in sighted controls (who do not heavily recruit the occipital cortex for Braille). Conversely, stimulating the VWFA in the blind might directly interfere with Braille reading if that region has taken on a critical function. Price and Devlin (2011) have similarly discussed using TMS to test top-down interactive models of reading. Demonstrating such causal interactions would strengthen the argument that occipital recruitment in the blind is driven by feedback from language areas.

Combining diffusion MRI tractography with functional task activation could clarify whether structural reorganisation in subcortical pathways correlates with differences in functional recruitment. Specifically, one could examine the connectivity of thalamic nuclei (e.g., lateral geniculate nucleus, pulvinar, medial geniculate) in congenitally blind individuals and test whether individuals with stronger pulvinar-to-temporal or medial geniculate nucleus-to-occipital structural connections show greater occipital activation during Braille reading (Marins et al., 2023). This would support the idea that the thalamus helps "re-route"

tactile or auditory information to occipital areas in blindness. Conversely, comparing these results with a dataset that found no significant thalamic changes (Reislev et al., 2017) can help identify whether perhaps only a subset of blind individuals (or specific methods) show such reorganisation. Multimodal imaging within the same individuals (Diffusion tensor imaging and fMRI) would allow us to link structure and function directly: for example, do blind individuals with intact lateral geniculate nucleus-to-occipital anatomical tracts perhaps use occipital cortex *less* for language (suggesting that if the visual pathway remains anatomically intact, it might somehow compete with or reduce cross-modal reorganisation)? Or, more likely, do all congenitally blind people rely on the occipital cortex for Braille reading regardless of whether gross thalamocortical anatomy has changed, implying that functional plasticity can bypass even an unchanged anatomical pathway? Such studies would deepen our understanding of how profoundly deprivation rewires the brain's information highways, and whether occipital language function in blindness requires physical "rewiring" or can arise from functional repurposing of existing circuits.

To tease apart critical periods from purely training-driven effects, future research should include groups of early-blind (congenitally blind), late-blind, and sighted Braille readers in the same experiment. If resources permit, one could even train late-blind adults in Braille to see if their occipital cortex can be recruited, or if that opportunity has passed after the critical period of visual cortex development. We predict that congenitally blind readers will show the strongest occipital involvement (as in our study), late-blind Braille readers might rely more on alternative networks (perhaps more on frontal or parietal areas and less on occipital - more akin to the sighted pattern), and early-blind individuals (blind since early childhood but with some visual experience in infancy) might show an intermediate pattern. Bedny et al. (2011) provide evidence that the onset of blindness matters: people who became blind later in life do not activate the occipital cortex for language to the same extent as those who were blind from birth. Testing such groups on Braille tasks would extend those findings into the literacy domain. It would also help isolate what aspects of the network are due to deprivation (sensory experience) versus Braille learning per se. For example, if late-blind Braille readers (who learned Braille in adulthood after losing sight) do activate occipital cortex for Braille, that would show that plasticity for Braille can occur even after a period of visual experience, purely via intensive training - but if they do not, it underscores the importance of early-life cross-modal development. Additionally, a within-subject longitudinal approach (e.g., following sighted trainees beyond 7 months of training, or tracking newly blind individuals as

they learn Braille) could reveal how training and deprivation effects accumulate or interact over time. Our cross-sectional design provides a snapshot; longitudinal studies would provide a trajectory, together forming a complete picture of when and how the brain adapts to tactile literacy.

8. General discussion and conclusions

8.1. Summary

Our findings demonstrate experience-dependent brain plasticity in adult learners, aligning with contemporary models that view the adult brain as dynamic and capable of reorganisation given appropriate training and sensory demands (Milbocker et al., 2024). The longitudinal results showed clear functional recruitment within just a few months of Braille training, reinforcing the idea that the adult cortex is not rigidly fixed after critical periods but can be significantly remodelled by new learning (Legault et al., 2019; Lehmann et al., 2023; Marie et al., 2023). This supports frameworks of adult plasticity in which training can induce functional reweighting of networks in task-relevant regions (Kao et al., 2020). For example, Braille learners exhibited increasing activation in somatosensory, occipital, and frontal areas with training, accompanied by performance gains, consistent with the idea that “neurons that fire together, wire together” to form new functional assemblies for the novel skill. This rapid onset of reorganisation is consistent with studies of other skills (e.g., motor learning), where structural and functional plasticity can be detected within days of practice (Stee et al., 2023). Crucially, our work extends plasticity models by detailing how the brain’s engagement shifts from “broad and effortful” to “focused and efficient” as a new skill is acquired (Bassett & Mattar, 2017; Yeatman et al., 2024). Early in training, Braille processing elicited widespread activation across bilateral fronto-parietal “multiple-demand” networks and subcortical structures, reflecting a heavy reliance on domain-general resources (attention, working memory, sequence processing) when the task was novel. This finding aligns with the scaffolding hypothesis in skill-learning models, which posits that novices recruit large, diffuse networks (especially executive control regions) to support performance before task-specific circuits are fully developed (Bassett & Mattar, 2017). Here, this was evident in the early activation of the dorsolateral prefrontal cortex, anterior cingulate/insula, and superior parietal cortex during initial Braille exposure: regions associated with adaptive cognitive control and salience detection (Molnar-Szakacs & Uddin, 2022). Additionally, engagement of the basal ganglia (putamen/caudate) and cerebellum was observed early on, aligning with models suggesting that subcortical loops contribute to action selection and sequence learning during initial skill acquisition (Roth & Ding, 2024). This broad activation profile in Braille learners closely mirrors patterns seen in other adult learning domains (e.g., learning a second language or complex motor sequences), supporting the idea of common, modality-general neuroplastic responses to new cognitive challenges (Wolna et al., 2024). As

training progressed, however, we observed a marked narrowing and task-specific concentration of brain activity: activation became more left-lateralised and focused in core language/reading regions (fusiform gyrus, inferior frontal gyrus, superior temporal areas), while diffuse bilateral and subcortical activations subsided, precisely what interactive scaffolding-to-specialisation models predict as novices become more automated and efficient (Turker et al., 2025). The fact that many of these fMRI-observed changes persisted even after a multi-week break in practice (with performance remaining above baseline) indicates at least partial consolidation, consistent with models in which continued maintenance of changes occurs during the time between sessions when no practice happens (Buch et al., 2021). This persistent reorganisation underscores the stability of adult learning-induced plasticity: once formed, the functional changes are not merely transient hyperactivations; they reflect lasting reconfigurations that can be re-engaged when the skill is resumed (albeit with some decay in strength without practice) (Leech et al., 2022).

Our findings also highlight the breadth of cross-modal plasticity in adults. Prior sensory deprivation research has shown that blind individuals repurpose their “visual” cortex for touch and hearing, and short-term blindfolding in sighted people can induce occipital responses to touch (Lo Verde et al., 2017; Müller et al., 2019; Norman et al., 2024). We extend this by demonstrating that sighted adults, even those with normal vision, can develop new tactile-language integrations. With training, touch starts to engage not only somatosensory areas but also higher-level occipito-temporal areas typically used for visual reading (Y.-F. Liu et al., 2023; Tian et al., 2023). This speaks to a fundamental capacity for cross-modal recruitment under task-specific constraints: when a behaviour (like reading) places new demands on the system, the brain will recruit whatever circuits can help meet those demands, even if it means “borrowing” cortical territory usually devoted to another sense (W. J. Park & Fine, 2024). Indeed, we observed that after several weeks of Braille learning, sighted participants showed reliable engagement of the VWFA during tactile reading, indicating that the visual-stream cortex had become incorporated into the tactile reading network. This cross-modal functional plasticity in sighted adults aligns with evidence from sensory substitution, where visual areas can acquire new roles given appropriate top-down associations (Damera et al., 2023). In the context of plasticity theories, these results reinforce an experience-driven connectivity account: cortical regions are not irrevocably tied to their original inputs, but can be reassigned based on patterns of co-activation and long-range connectivity (J. Li et al., 2020; Yablonski et al., 2024). At the same time, the

limits of this brain reorganisation are evident: sighted learners did not uniquely activate the primary visual cortex (V1) for Braille, unlike congenitally blind readers, who do recruit V1 for touch, consistent with hierarchical constraints whereby early sensory cortices in sighted adults remain engaged by vision (Pang et al., 2024; Sadato et al., 1996). In contrast, higher-level visual areas (vOTC), which have strong connectivity to language networks, are more adaptable to new input integration (Dębska et al., 2023). Overall, our study confirms that adult plasticity, while not boundless, is remarkably sufficient to support the acquisition of a complex new skill (tactile literacy) and to reorganise both cortical and subcortical circuits in the process (Kogan et al., 2023; Roth & Ding, 2024).

8.2. Models of neuroplasticity

Taken together, our data indicate that adult literacy learning in a new modality is governed by task-centric, connectivity-constrained plasticity: across print, visual Braille, and tactile Braille, a modality-independent core repeatedly engaged the left IFG and VWFA, consistent with proposals that connectivity biases scaffold where orthographic processing emerges. (Hannagan et al., 2021; Saygin et al., 2016). Longitudinally, Braille training in sighted adults followed a scaffolding-to-specialisation trajectory: early sessions elicited broad bilateral multiple-demand and sensorimotor recruitment for effortful, serial exploration, which narrowed with practice to a left-dominant network centred on IFG/vOTC, and remained partly stable after a practice hiatus, consistent with consolidation dynamics (Shashidhara et al., 2024; Yang et al., 2025). Mechanistically, the pattern aligns with interactive/predictive accounts: co-activation of IFG with VWFA during Braille reading supports top-down constraints on orthographic representations. At the same time, subcortical loops contribute to sequence learning and automatisisation, basal ganglia and thalamus shaping sequencing/selection, and the cerebellum supporting timing and automatised skill (Chauhan et al., 2024; Jobson et al., 2024; Klostermann & Tiedt, 2023). Critically, automaticity emerged: in a tactile detection task without explicit reading demands, learners (but not controls) recruited reading-relevant cortex alongside premotor-parietal and subcortical nodes, indicating that once symbol-language mappings are established, incidental Braille input can trigger the reading network by default, paralleling observations that VWFA-language coupling strengthens when engaging in word recognition (White et al., 2023). At the same time, sensory experience conditions plasticity. Congenitally blind readers showed stronger occipital and occipitotemporal participation (including classically “visual” territories) during Braille than sighted learners, who relied more on frontoparietal scaffolding; thus, blindness

favours occipital integration into language/executive networks, whereas in sighted adults, primary visual cortex remains largely vision-bound while higher-level VWFA adapts to tactile input (Kanjlia et al., 2021; Tian et al., 2023). Together, these results refine contemporary models. First of all, reading organisation is fundamentally metamodal at the IFG-VWFA level, provided experience establishes symbol-language mappings (Dębska et al., 2023; Tian et al., 2023). Secondly, learning progresses from broad control scaffolds to focused language specialisation, with durable (though practice-supported) retention (Buch et al., 2021; Shashidhara et al., 2024). Third, predictive, cortico-subcortical loops scaffold emergent automaticity (Klostermann & Tiedt, 2023; White et al., 2023). Finally, experience-driven connectivity and hierarchy set the bounds; vOTC is pliable in adulthood, whereas the early sensory cortex is repurposed chiefly when visual experience is absent (Saygin et al., 2016; Tian et al., 2023).

8.3. Limited sample sizes and the specificity of the cohort

Our longitudinal training study and implicit reading experiment involved 17-20 participants in each group (young adult females in the experimental and control groups). Such samples are comparable to recent neuroimaging on numerical cognition in sighted Braille readers (Czarnecka et al., 2023; Rączy et al., 2020). Related work from Collignon's group shows that arithmetic engages reorganised occipital circuits in congenital blindness and that basic numerical abilities emerge without visual experience, underscoring domain relevance (Crollen et al., 2021; Crollen & Collignon, 2020). Nevertheless, modest samples reduce power for small effects and individual-difference moderators (Kang et al., 2024; Marek et al., 2022). The cross-sectional comparisons are additionally limited by unmatched age and sex distributions: the blind group was older and mixed-sex, whereas the sighted groups were younger and female-only. These factors do not explain the entire anatomical pattern, but they limit any single-factor attribution of group differences.

8.4. Task design and ecological validity

We used lexical decision and dot-detection paradigms rather than naturalistic comprehension tasks. These well-controlled tasks are standard in neuroimaging, yet they simplify everyday reading and may under-engage processes such as discourse-level semantics (Nastase et al., 2020; Turker et al., 2025). Moreover, although we debriefed participants and found no overt awareness of embedded words in the implicit task, some residual awareness cannot be ruled out (Kiefer et al., 2023). Future work can incorporate online awareness probes or utilise rapid

presentation to constrain awareness, and include sentence- or paragraph-level tasks to enhance ecological validity (Shain et al., 2020).

8.5. Control group and potential confounds

Our passive control group did not receive an alternative training. This isolates the effects of Braille training but raises concerns about group differences in engagement or expectations, which are known to bias training outcomes (Boot et al., 2013). Active tactile-training controls (e.g., texture identification or a non-linguistic tactile code) would better dissociate orthography-specific changes, such as VWFA-related effects, from generic tactile practice, because non-linguistic tactile tasks predominantly recruit somatosensory-parietal systems rather than orthographic-language circuits, and VWFA subregions show distinct connectivity to visual vs language networks (Yablonski et al., 2024). Including late-blind learners longitudinally would also test how sensory experience shapes plasticity trajectories across occipital and higher-order networks (Mattioni et al., 2022; Saccone et al., 2024).

In summary, while our research supports adult cross-modal plasticity and a largely modality-independent reading network, it does so under specific conditions (intensive Braille training in young, highly educated, sighted adults). Converging evidence indicates that reading circuits are constrained more by network organisation than by input modality (J. Li et al., 2022). At the same time, adaptability has limits: in sighted learners, primary visual cortex typically retains domain specialisation, whereas nonvisual recruitment of occipital cortex is far more characteristic of congenital blindness, consistent with sensitive-period effects (Kanjlia et al., 2021; Musz et al., 2022). Nonetheless, our core observations: VWFA engagement during tactile reading, durable training-related brain changes, and emergent automaticity, were consistent across participants (Matuszewski et al., 2021; Yeatman & White, 2021).

8.6. Conclusions

This dissertation shows that adult Braille learning recruits a shared reading-related network across tactile and visual input, while preserving clear modality- and experience-dependent differences in its broader implementation. In sighted adults, Braille training was associated with early IFG recruitment, later left vOTC engagement, and durable changes that remained above baseline at follow-up. Across print, visual Braille, and tactile Braille, left IFG and vOTC were consistently recruited, alongside modality-specific sensory and sensorimotor extensions. In a non-linguistic tactile detection task, Braille learners showed stronger

reading-relevant network engagement than passive controls despite similar behavioural performance. Congenitally blind readers shared part of this higher-level network but showed stronger occipital recruitment than sighted learners, indicating that sensory experience shapes how tactile reading is implemented. Together, these findings support a shared reading-related core across modalities.

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Publications of the PhD Candidate

- Olszewska, A. M., **Gaca, M.**, Drożdziel, D., Jednoróg, K., Marchewka, A., & Herman, A. M. (2025). Piano training induces dynamic neuroplasticity of bimanual coordination but not auditory processing in young adults. *Journal of Neuroscience Research*, 103(7), e70067. <https://doi.org/10.1002/jnr.70067>
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