Neuropsychologia 190 (2023) 108685

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Rapid plasticity in the ventral visual stream elicited by a newly learnt auditory script in congenitally blind adults

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ARTICLE INFO

Keywords:
fMRI
Visual deprivation
Reading
Sensory substitution device
Blindness
Plasticity

ABSTRACT

Accumulating evidence in the last decades has given rise to a new theory of brain organization, positing that cortical regions are recruited for specific tasks irrespective of the sensory modality via which information is channeled. For instance, the visual reading network has been shown to be recruited for reading via the tactile Braille code in congenitally blind adults. Yet, how rapidly non-typical sensory input modulates activity in typically visual regions is yet to be explored. To this aim, we developed a novel reading orthography, termed OVAL, enabling congenitally blind adults to quickly acquire reading via the auditory modality. OVAL uses the EyeMusic, a visual-to-auditory sensory-substitution-device (SSD) to transform visually presented letters optimized for auditory transformation into sound. Using fMRI, we show modulation in the right ventral visual stream following 2-h of same-day training. Crucially, following more extensive training (i.e., ~12 h) we show that OVAL reading recruits the left ventral visual stream including the location of the Visual Word Form Area, a key graphene-responsive region within the visual reading network. Our results show that while after 2 h of SSD training we can already observe the recruitment of the deprived ventral visual stream by auditory stimuli, computation-selective cross-modal recruitment requires longer training to establish.

1. Introduction

Classic theories of sensory brain organization propose that each sensory modality is processed by a distinct cortical region. Visual inputs are processed in the occipital cortex, auditory inputs in the temporal cortex, and tactile perception in the fronto-parietal cortex (Pandya et al., 2015). However, accumulating evidence in the last two decades challenges these classical views, indicating that sensory cortices could be recruited by non-typical modalities (Heimler and Amedi, 2020).

Studies on sensory-deprived individuals such as congenitally blind adults revealed that deprived sensory cortices maintain their selectivity to process specific computations even when such computations are carried out by atypical, yet intact sensory modalities. For example, the lateral occipital complex in the visual cortex of blind individuals has been shown to process objects via tactile exploration (Amedi et al., 2010). Similarly, tactile Braille reading engages the left Visual-Word-Form-Area (VWFA) (Reich et al., 2011).

These findings led to the development of a Task-Specific Sensory-Independent (TSSI) theory of brain organization. This theory proposes that brain regions previously considered visual are in essence multimodal, processing specific computations and tasks regardless of the sensory modality used as input. This implies that category-selective regions in the ventral visual stream might respond to specific, sensory-independent shape-patterns rather than visual-only features (Heimler et al., 2015).

A consistent bulk of evidence supporting this theory comes from studies using Sensory Substitution Devices (SSDs) that convey shape-related inputs via non-typical sensory modalities to congenitally blind adults. SSDs translate information typically perceived via one sensory modality to a non-typical sensory modality. An example is the EyeMusic SSD, a visual-to-auditory device that uses sounds to represent images in a shape and color preserving manner (Abboud et al., 2014). Using the sweep-line technique, an image is scanned from left to right, and each pixel of the image is translated to a musical note using a dedicated algorithm that maintains both color and location features of the image using time, sound-frequency, and musical timber. Using the EyeMusic

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https://doi.org/10.1016/j.neuropsychologia.2023.108685
Received 15 September 2022; Received in revised form 7 August 2023; Accepted 20 September 2023

SSD, as well as other similar visual-to-auditory SSDs (Meijer, 1992), congenitally blind participants were trained for an extensive amount of hours, (e.g., >70 h overall in recognizing through the auditory modality various categories of objects. Then, they were scanned using functional magnetic resonance imaging (fMRI) while presented with SSD objects belonging to the trained "visual" categories (Abboud et al., 2015; Striem-Amit et al., 2012b; Striem-Amit and Amedi, 2014). These studies showed that after extensive training with SSD, the deprived ventral visual cortex was recruited by auditory stimuli maintaining its functional selectivity. Specifically, these works showed TSSI organization for the left VWFA processing SSD-conveyed letters (Striem-Amit et al., 2012b), for the extrastriate body area processing SSD-conveyed body shapes (Striem-Amit et al., 2012) and for the number form area when processing SSD-conveyed numbers (Abboud et al., 2015).

Crucially, one important open question is how rapidly these regions can re-purpose to process a computation using a novel sensory input. There is only one study addressing this question focusing on large-scale TSSI division of labor between dorsal and ventral streams and showing that such division occurred after less than 2 h of training (Striem-Amit et al., 2012). How long it takes for TSSI computation-selectivity to be established for specific object categories was not yet investigated.

To address this question, we reasoned to first focus on the reading system. One unique characteristic of reading differentiating it from other groups of visual object categories, is the fact that it is a new human ability in evolutionary terms, and as such, its cortical representation cannot be driven by forces of evolutionary adaptation solely (Dehaene and Cohen, 2007). Thus, the cortical representation of reading is thought to arise from the "recycling" of existing cortical maps enabling similar computations, making the neural reading system highly adaptable (Dehaene and Cohen, 2007). Furthermore, the reading system has been shown to adapt to acquired literacy even when it occurred in adulthood, suggesting lasting plasticity (Dehaene et al., 2010). Therefore, we hypothesize that the reading system may be the quickest visual system to adapt to novel input, offering an ideal study model for rapid specialized neural plasticity.

To this aim, we first conducted a same-day pre-post-training paradigm interleaved by 2-h of dedicated reading training using a novel auditory script based on visual-to-auditory SSD. Specifically, we taught a group of congenitally blind adults to identify letters and read short words composed of a novel orthography, termed OVAL. In the OVAL auditory script, each letter is represented by a specific auditory sound, based on a visual combination of vertical lines and dots, as well as a specific color represented by timber. The OVAL script relies for such transformation on the algorithm of the EyeMusic SSD (Abboud et al., 2014). Participants learn to decipher the spatial combination specific to each letter as well as its assigned color, via a tailored training program. Previous work led by the authors has shown that OVAL is easy to learn and that following the program, participants are able to easily discriminate OVAL letters and read short words composed of them. (for a detailed description of OVAL and its learning in blindfolded adults, see (Arbel et al., 2020). Using fMRI scans before and after 2-h of same-day OVAL learning, we investigated which regions would rapidly adapt to decode this newly learned orthography. We then continued training with OVAL for ~12 additional hours and compared OVAL reading with other visual categories, to investigate dynamics of neural recruitment following more prolonged training. One possibility is that very short training will result in non-specific recruitment of visual regions, or even high-order association areas, followed by more refined recruitment of word- and reading-related regions after more prolonged training. Another possibility is that even following such short-duration training, task specific recruitment of word- and reading-related regions will occur.

A second aim of the present study was to provide quantitative assessment of OVAL reading in congenitally blind adults, to validate its feasibility for literacy acquisition in blindness. While the tactile Braille code is the most prevalent reading system for reading by blind individuals, the alarming decrease of Braille usage results in lower literacy rates among blind individuals (Scheithauer and Tiger, 2012). Considering the far-reaching consequences of illiteracy, on both social factors as well as development of broad neural networks known to be mediated by literacy acquisition (Ryles, 1996; Silverman, Arielle Michal; Bell, 2018), cheap and easy-to-learn reading methods are required for reading rehabilitation in the blind. Here we thus present OVAL reading ability achieved by congenitally blind adults, using the same reading tasks validated previously in a group of blindfolded sighted (Arbel et al., 2020).

2. Material and methods

2.1. Participants

A total of 11 congenitally blind individuals took part in the presented experiments (age: 37.27 years SD: 5.26, Table 1). All participants were literate, native Hebrew speakers without any diagnosed neurological conditions. In addition, all participants were expert users of the EyeMusic or other visual-to-auditory SSD, and had >50 h of SSD training, as part of a longitudinal study conducted in the lab. The Hadassah Medical Centre Ethics Committee approved the experimental procedure; written informed consent was obtained from each participant. Participants were reimbursed for their participation in the study.

2.2. OVAL system

The OVAL auditory script is a novel alphabetic orthography designed for compatibility with the EyeMusic visual-to-auditory sensory substitution device (SSD). Each letter of the alphabet is created in its visual form using a unique combination of vertical lines and dots, which vary in number as well as in their spatial layout, and color (see for additional details (Arbel et al., 2020)). OVAL letters are transformed to sound following the three principles of the EyeMusic SSD: 1. Y-axis location: the higher on the screen a feature of a character is positioned, the higher in pitch it will be sonified, and the lower on the screen a feature of a character is positioned, the lower in pitch it will be sonified, using a pentatonic scale; 2. X-axis location: each image is scanned from left to right in a column-by-column manner, so that users will hear first the feature of a character positioned more to the left. 3. Color: 5 Colors are conveyed via 5 music instruments. , thus color served as another feature helping to differentiate among the letters (Arbel et al., 2020).

OVAL characters are composed by combining together features from Braille system and Morse code. Letter orthography was based on the same combination of dots and lines as in Morse code. However, differently than Morse code, in OVAL, lines were vertical rather than horizontal to take advantage of pitch variations characterizing the EyeMusic algorithm and thus potentially facilitate the letters' differential perception. This choice also allowed each character to be played more quickly than if horizontal lines were used. (see (Arbel et al., 2020) for a detailed account on the OVAL script).

2.2.1. Experimental procedure

First, to investigate rapid-recruitment for a script conveyed via a non-typical sensory modality we conducted a same-day pre-post-training paradigm. On the first day of OVAL training, participants had a "pretest" fMRI scanning session, as described below in the section below, followed by 2 h of OVAL training, and second "post-training" scanning session. Second, to provide quantitative reading measures for the OVAL script in blind, we also tested a group of congenitally blind individuals on a letter identification task and word reading task following 6 h of OVAL acquisition. These tasks were identical to those validated on blindfolded sighted individuals (Arbel et al., 2020). Third, in addition to testing rapid plasticity, we further investigated neural mechanisms mediating OVAL reading following more prolonged training, and their comparison to a traditionally right-lateralized category of objects

Table 1
Demographic details of participants.

participant	age	blindness cause	light perception	age at blindnes onset	Braille reading	handedness	Part I: rapid plasticity	Part II: OVAL reading	Part III: prolonged plasticity
DH	37	Retinopathy of prematurity	no	0	yes (since age 4)	right	V		
FO	32	Microphthalmia	No	0	yes (since age 5)	right	V		V
ElMa	35	Retinopathy of prematurity	no	0	yes (since age 5)	right	V		
FH	41	Leber's Disease	faint	0	yes (since age 5)	ambidextrous	V	V	V
NN	44	Retinopathy of prematurity	No	0	yes (since age 6)	right	V	V	V
PC	40	Retinopathy of prematurity	No	0	yes (since age 6)	right	V	V	V
PH	41	Rubella	no	0	yes (since age 5)	right	V		V
FN	32	Leber's Disease	Faint	0	yes (since age 5)	ambidextrous		V	V
DS	33	Retinopathy of prematurity	No	0	yes (since age 6)	right		V	V
UM	38	retinoblastoma	no	3	yes (since age 4)	ambidextrous		V	
HB	26	anophthalmus, fall	No	<1	yes (since age 4)	left		V	

identified on the exemplar level - faces. For this aim participants continued to train on OVAL reading using additional words and sentences, for up to 12 h. In addition, participants underwent a parallel training program on face perception, for comparable duration of OVAL training. (For a details account on face-training program see (Arbel et al., 2022). Lastly, and to provide control for the body-related task of face perception, participants learned to identify hand gestures using EyeMusic. Following this more intense training program consisting of additional visual categories, participants underwent a final fMRI experiment. This experiment compared neural recruitment for word reading in comparison to these two additional categories.

All behavioral experiments were performed using Presentation® software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com).

2.3. Part I: rapid modulation for OVAL learning

Pre-post-training Block-design fMRI experiment: In order to isolate the neural network that is modulated by auditory letter recognition acquisition, we conducted a pre-post block design experiment, which was first ran before any training, and again following 2 h of OVAL training, as follows: We conducted a block-design experiment using 3 different sets of letter stimuli that were introduced in four conditions: *a. Trained letters - letter identification,* 3 letters participants learned to

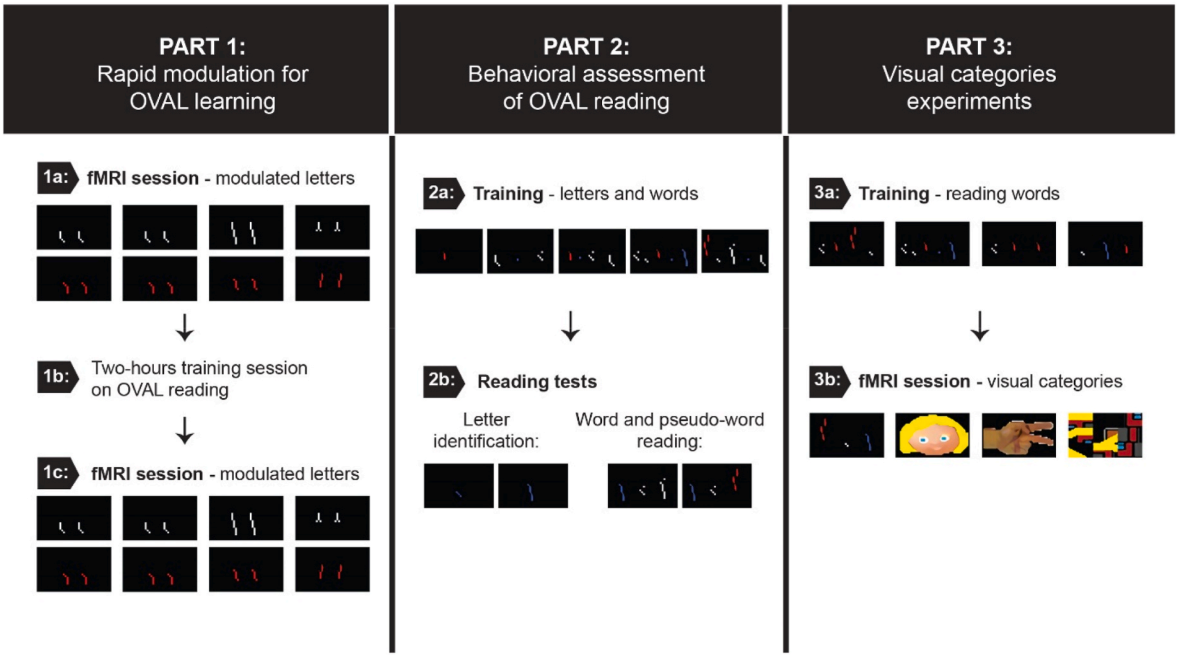


Fig. 1. Experimental paradigm. The experiment was divided into three parts. First, to test rapid neural modulation for a novel script, participants underwent an fMRI session before and after 2 h of OVAL training (Part I). Second, participants were tested on letter identification and word reading, following several more hours of OVAL training (Part II). Third, to test neural modulation following more training, participants were tested using fMRI again after 6 more hours of OVAL training (Part III).

identify during the 2-h training, *b. Trained letters - color identification*, the same three letters from condition a *c. Pseudo-letters,* 3 untrained letters with visual similarities in both shapes and colors to the letters in conditions a and b, *d. false-font,* scrambled visual representations of trained letters [Fig. 1]. The resulting images were sonified via EyeMusic.

The conditions were presented in a block design paradigm. The experiment was programmed using Presentation software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Each condition was repeated 6 times, in a pseudorandom order, for a total of 24 blocks. To increase data robustness, we collected data over 3 runs using the following design: In each block, 4 different stimuli belonging to the same experimental condition were displayed, each stimulus repeated twice consecutively for a total time of 1.5 s, followed by a response interval of 1.5 s. Each block lasted 12 s. Each block started with an auditory cue indicating the tested category which lasted for 2 s (trained letters; color; pseudo-letters; false-fonts), and was followed by a rest interval of 10 s. Participants were instructed to listen carefully to the soundscapes and to provide their responses using a response box after the end of both repetitions of a stimulus. In condition a, participants were instructed to identify the letter. In condition b, participants were instructed to identify the color. Importantly, the response mapping for condition a and condition b were different, such that different fingers were used to identify the letter in condition a, and its color in condition b, to ensure that participants were not explicitly using only color information in condition a or shape information in condition b. For untrained and scramble letters (thus un-identifiable even after training), participants were instructed to closely attend the auditory stimuli and press randomly as motor control at the end of the stimulation. The experiment was ran first before any explanation about the OVAL alphabet, and again following 2 h of OVAL training. Since before any OVAL introduction participants were unable to identify letter, to control for motor response, participants were instructed to attend to all stimuli, try to decipher their shape and sound, and provide a random key press.

Before entering the scanner, participants were familiarized with the tasks inside the scanner especially for what it concerns the response box, to make sure the response mapping was fully understood by all. Digital auditory soundscapes were generated on a PC, played on a stereo system, and transferred binaurally to the subjects through a pneumatic device and silicone tubes into commercially available noise shielding headphones.

2.4. Two-hour OVAL learning session

The OVAL training protocol was designed to teach participants the identification of 11 Hebrew OVAL letters (i.e., half of the Hebrew alphabet), using the EyeMusic SSD and read short words and pseudowords consisting of those letters formed by up to 5 characters. The training that took place during this session, follows the same training protocol detailed in (Arbel et al., 2020). Specifically, following the first fMRI session, it was explained to the participants that the sounds they just heard conveyed letters in a novel auditory orthography. Then, the training on reading with OVAL unfolded as follows: First, the letter "waw", the most common letter in the Hebrew orthographic system, was played. This is represented by a single blue dot in the OVAL orthography, translated into audition, according to the EyeMusic algorithm, as a brief, single tone played via the brass instrument. Participants, who were already expert EyeMusic users, were then encouraged to decipher such patterns independently, based on the algorithm of the EyeMusic. Most participants could report that the sound they heard represented a blue dot. The experimenter then provided participants with the phonological meaning of the audeme. The next letter, "alef" was then played. Again, participants tried to decipher the pattern based on the algorithm transformation rules with feedback from the experimenter if needed. The phonological meaning of the audeme was provided. Two more letters were introduced, and after a short repetition of the first 4 learnt OVAL letters, participants were instructed to read short words composed of these characters. When participants became able to read these words, 3 more letters were introduced following the same procedure described above, then participants were asked to read words formed by any combination of the 7 letters they learned. Then 2 more OVAL letters were introduced, and then participants read words composed by any of the 9 letters learned; then the 2 last letters were added and participants read words composed by any of the 11 learned letters. The final part of the training consisted of reading words and pseudo-words containing all 11 learned letters. Within this first 2-h session, between the pre- and post-training fMRI session, the majority of participants learned 7 OVAL letters (and to read short words composed by them). The final 10 min of the session were dedicated to the understanding of the finger-mapping in the fMRI session, and repeating the 3 experimental trained letters (Dalet, Het, and Tzade), as well as the finger-mapping for the color condition.

2.5. Part II: Behavioral assessment of OVAL reading

To assess OVAL reading in congenitally blind and to validate its feasibility as a literacy option for the blind population, we tested a group of seven congenitally blind on OVAL reading following 6 h of OVAL training, using the same approach tested on blindfolded adults (Arbel et al., 2020). In brief, OVAL instruction was as detailed above, and was followed with 2 additional sessions of 2 h each, in which participants completed training on half of the Hebrew alphabet and practiced words and pseudo-words composed of these letters. After completing 6 h of OVAL learning participants were tested on two reading tests.

2.5.1. Behavioral experiment 1 - letter identification of trained characters

In order to test basic letter identification ability following training, participants were asked to name each of the 11 experimental letters they received training on. Each trial began with a silence period of 1500–1800 ms and then 1 OVAL letter was presented repeatedly within 4 s intervals (i.e., the time used by the EyeMusic to scan each OVAL display). Participants were instructed to press the space bar as soon as they identified the letter and then to give their response orally (which was inserted in the computer by the experimenter). Then they pressed again the space bar to move to the next trial. During the experiment, each letter was repeated 6 times for a total of 66 trials in a random order with the constraints that the same letter could not be repeated more than twice consecutively, and that repetitions of the same letter were not all appearing in the same chunk of the experiment. There were two possible trials sequences to control for order biases, which were presented to participants in counterbalanced order. The number of correctly identified letters (correct rate – CR) and reaction times were collected. The experiment lasted ~10 min.

2.5.2. Behavioral experiment 2 – words/pseudo-words reading task

To test participants' reading proficiency, after training, they underwent a words/pseudo-words reading task. 68 stimuli, half words and half pseudo-words with various length, all of which had not been introduced during training, were presented in a random order, with the constraints that not all same-length words appeared in the same chunk of the experiment. Pseudo-words were created by switching one letter of an experimental word, with a different letter from the pool of trained letters. Each word/pseudo-word consisted of two to five letters (20 short words and 20 pseudo-words of either 2 or 3 letters; 14 long words and 14 long pseudo-words of either 4 or 5 letters, using all the 11 characters learned during training). Each stimulus was played repeatedly until participants' response. Participants were informed at the beginning of the task that stimuli could be either words or pseudo-words and were instructed to listen to the whole stimulus and press the space-bar as soon as they completed the reading of each word/pseudo-word. Then they were asked to provide their response orally, namely saying the word/pseudo-word aloud (and the experimenter entered it in the computer) and pressed the space bar to move to the next trial. Each trial started with a tone marking its beginning lasting ~20 ms. During the experiment, each word/pseudo-word was presented within 4 s intervals (i.e., the time used by the EyeMusic to scan each OVAL display). The number of correctly read words/pseudo-words (CR) and reaction times were recorded. The length of the experiment varied based on participants' performances, ranging between 20 and 40 min.

3. Data analysis

All statistical analysis for behavioral tests was conducted using JASP software (version 0.14), using t-tests against chance level, and mixed repeated measures ANOVA. Reaction times calculated for the 'letter identification' and 'word reading' tasks are calculated only for correct trials. In all reported data, data is presented as a mean, followed by ± standard deviation.

3.1. Part III, Visual categories experiments

3.1.1. Training

7 participants (5 of whom also participated in Part I above) continued training on OVAL reading. After completing the basic protocol consisting of 6 h of training, participants had additional 2–3 sessions of 2-h each, with additional word training before the fMRI session. In addition, during this part of training, participants also read word combinations, sentences and even paragraphs composed of the trained letters. In parallel participants underwent face training and hand-gestures training (For a detailed account on face-training program see (Arbel et al., 2022). In brief, face-training focused on teaching congenitally blind adults the perception and identification of colorful cartoon faces, conveyed via the SSD. Training focused on teaching participants the composition of faces, and how to perceive the complicated auditory soundscapes, using 6 cartoon faces adapted from the children's' game "Guess Who". Hand-gestures included soundscapes of hands representing hand gestures of "rock", "paper", and "scissors".

3.1.2. fMRI experiment

Stimuli from 3 categories were included. **Written words:** soundscapes of three 3-letter words presented in the OVAL orthography. **Faces:** soundscapes of the three male trained characters learned during face-training. **Hands' gestures:** soundscapes of three trained hands' gestures were included in the experiment taken from the paper-rock-scissors game: a hand featuring the gesture of a "rock" (fist), a gesture of "paper" (open hand) and "scissors" (two straight fingers, other fingers in a fist). **Scramble:** 3 soundscapes of scrambled colorful images of houses as control stimuli. The experiment was programmed using the "presentation" software and was presented in a block design paradigm:

In each block, 2 different stimuli of the same condition were presented, each lasting 5 s (two consecutive repetitions of a 2.5 s per stimulus), followed by a response interval of 2 s. Each block started with an auditory cue indicating the tested category (faces; words; hands' gestures; scramble) which lasted 2 s. All blocks lasted 16s and were followed by a 10s rest interval. Participants were instructed to identify each stimulus and provide their responses using a response box after listening carefully. Before entering the scanner, all participants were familiarized with the stimulus-finger mapping. For the "scrambled" condition participants were instructed to press randomly, for a motor response.

3.1.3. Functional and anatomical MRI acquisition, for part I and II

BOLD fMRI measurements were obtained in a whole-body, 3–T Magnetom Skyra scanner (Siemens, Germany). Scanning session included anatomical and functional imaging. Functional protocols were based on multi-slice gradient echoplanar imaging (EPI) and a 20 channel head coil. The functional data were collected under the following timing parameters: TR = 2 s, TE = 30ms, FA = 70°, imaging matrix = 80X80, FOV = 24 × 24 cm^2 (i.e., in-plane resolution of 3 mm). 29 slices with slice thickness = 4 mm and 0.4 mm gap were oriented in −22deg from the axial position, for complete coverage of the whole cortex in minimization of artefacts from the frontal sinus. The first ten images (during the first baseline rest condition) were excluded from the analysis because of non-steady state magnetization.

High resolution three-dimensional anatomical volumes were collected using a 3D-turbo field echo (TFE) T1-weighted sequence (equivalent to MP-RAGE). Parameters were: Field of View (FOV) 23 cm (RL) x 23 cm (VD) x 17 cm (AP); Foldover-axis: RL, data matrix: 160x160x144 zero-filled to 256 in all directions (approx. 1 mm isovoxel native data), TR/TE = 2300ms/2.98ms, flip angle = 9°.

3.1.4. Pre-processing of fMRI data

Data analysis was performed using Brain Voyager QX 2.0.8 software package (Brain Innovation, Maastricht, Netherlands). fMRI data preprocessing steps included head motion correction, slice scan time correction, and high-pass filtering (cut-off frequency: 2 cycles/scan). No head movement beyond 2 mm was detected in the collected data, thus all participants were included in the subsequent analyses. Functional data underwent spatial smoothing (spatial Gaussian smoothing, full width at half maximum = 6 mm) to overcome inter-subject anatomical variability within and across experiments. Functional and anatomical datasets for each subject were first aligned (co-registered) and then transformed to fit the standardized Talairach space (Talairach and Tournoux, 1988).

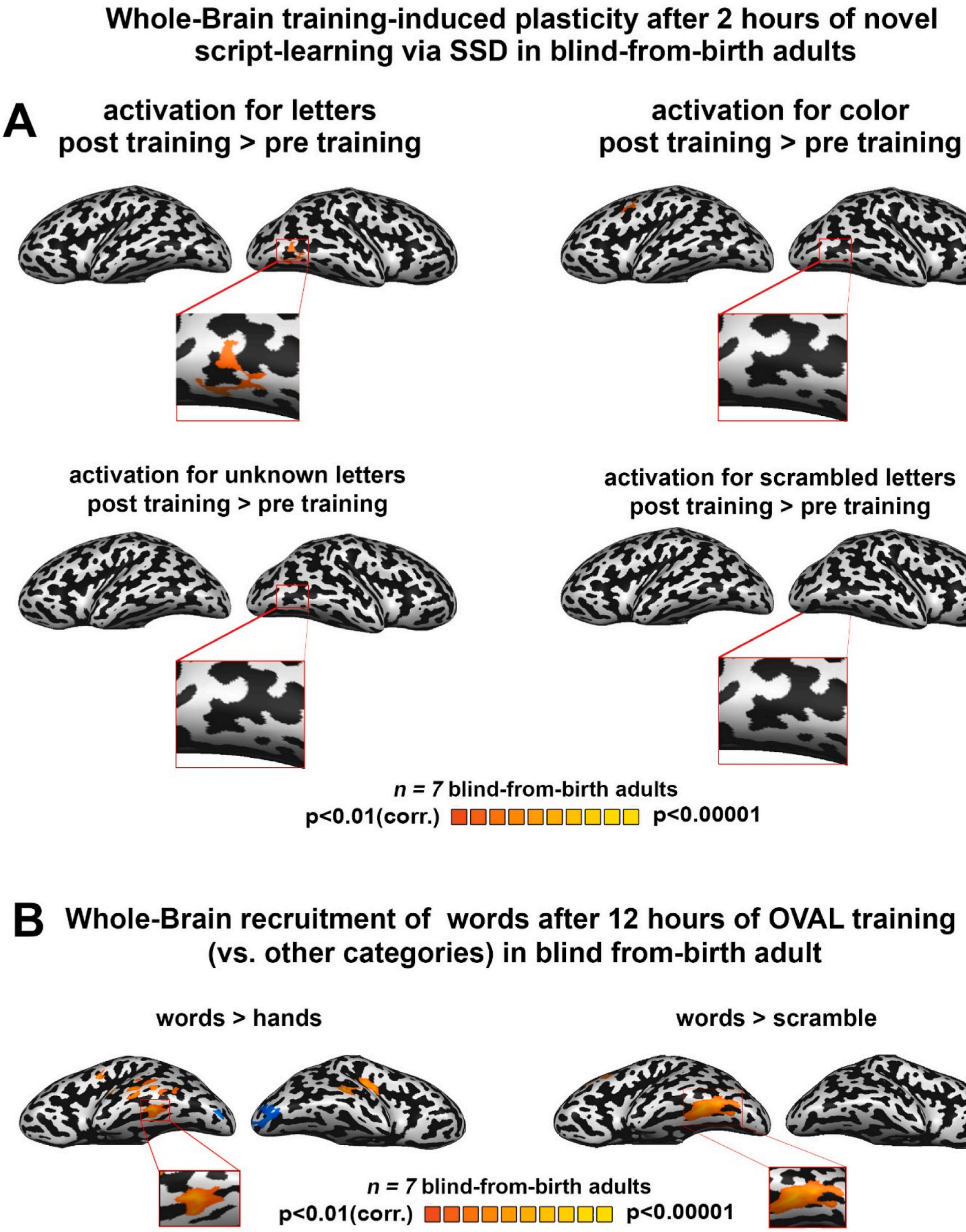
Whole-Brain GLM analysis. To compute statistical maps, we applied a general linear model (GLM) using predictors convoluted with a typical hemodynamic response function. Across-subject statistical maps were calculated using hierarchical random-effects model analysis (Friston et al., 1999). The minimum significance level of all results presented using GLM analysis was set to $p < 0.01$ before correction, and then corrected for multiple comparisons to $p < 0.05$ using a cluster-size threshold adjustment for Monte Carlo simulation approach extended to 3D datasets, using the threshold size plug-in Brain Voyager QX (Forman et al., 1995).

To test which regions show rapid recruitment for OVAL letter following 2-h of OVAL acquisition, we compared neural activation after training to neural activation before training, for each condition separately, using a whole-brain analysis RFX-GLM analysis as described above. Minimum cluster size after correcting for multiple comparison was 36 functional voxel. To test for neural recruitment for auditory OVAL reading following more intensive OVAL training we compared activation elicited to OVAL words with activation elicited to each other condition: faces, hands (minimum cluster size after correction 60 functional voxels) and scramble (minimum cluster size after correction 80 functional voxels).

4. Results

4.1. Part I: Right ventral visual stream modulation following 2-h of OVAL script acquisition

To examine neural modulation to 2 h of OVAL training, we tested congenitally blind adults on a task of letter identification before, and after 2 h of training. Whole-brain RFX-GLM analysis comparing neural response to OVAL letter identification following 2-h training, with activation for the same letters before training, shows a cluster encompassing the right lateral Fusiform gyrus extending to the inferior temporal gyrus with peaks at talairach coordinates: 46, −54, −2, (Inferior Temporal Gyrus) and 34–65 -15 (Fusiform Gyrus) (Fig. 2A). No other region outside the visual cortex shows modulation by training for letter identification. Investigation of modulation by OVAL training for the other conditions (color identification of trained letters, pseudo-letters and false font) with the same condition before training, revealed no training induced cortical modulation, of the right ventral visual stream nor any other brain region. For what concerns the "color" condition, as



Whole-Brain training-induced plasticity after 2 hours of novel script-learning via SSD in blind-from-birth adults

A

activation for letters post training > pre training

activation for color post training > pre training

activation for unknown letters post training > pre training

activation for scrambled letters post training > pre training

B Whole-Brain recruitment of words after 12 hours of OVAL training (vs. other categories) in blind from-birth adult

words > hands

words > scramble

Fig. 2. Rapid and prolonged training-induced neural modulation for a newly learned auditory script in congenitally blind adults, after 2 h and again after 12 h of training. A - After 2 h of OVAL training, we observed Training-induced plasticity in the right ventral visual stream only for OVAL letter identification (up left panel), and not for any other experimental condition, i.e., implicit letter identification (color condition) (up right panel), attention to pseudo-letters (bottom left panel) or false fonts (bottom right panel).

B - After 12 h of OVAL training, we observe a selective recruitment for OVAL words versus another visual category (hands' gestures) as well as for words versus the scramble condition in congenitally blind adults, in a location in the left hemisphere close to the Visual Word Form Area in the left Fusiform Gyrus - the typical node for reading localization.

participants were already proficient in identifying the colors presented by timbres using the EyeMusic before the 2-h OVAL training, this condition also served as an implicit letter recognition task. Thus, results indicated that implicit recognition of letters via an orthogonal behavioral task, was not enough to recruit the ventral visual stream.

4.2. Analysis of behavioral tasks during fMRI session

When analyzing participants' behavioral results during fMRI experiment following 2 h of OVAL training, we observed that participants where accurate in identifying the correct letter in 86.9% of the times (SD = ±23.62%) significantly above chance level (t (7) = 6.04, $p <$

0.001, $d = 2.28$), and the correct color 92.96% percent of the times (SD $= \pm 6.54\%$) significantly above chance level as well (t (7) $= 24.24$, $p < 0.001$, $d = 9.16$).

4.3. Part II: Recruitment of the left ventral visual stream including the VWFA for OVAL reading following 12 h of OVAL script acquisition

Following the completion of the basic reading instruction program, and following advanced word-reading lasting 6 more hours, participants were tested again using fMRI this time on word reading as well as two tasks of auditory category identification: faces and hand gestures as well as a scramble control condition. Whole-brain RFX analysis of words vs. scramble showed a significant cluster of activation in the left fusiform gyrus with peaks in (−43 -63 -11) and (−42 -50 -14) Talairach coordinates. Peak activation for OVAL reading was near that reported previously for visual reading (TC -42, −57, −6 (Cohen et al., 2000)) (Fig. S1a). The contrast of words with hands shows a cluster in the anterior fusiform gyrus with peak at (-40 -42 -10) Talairach coordinates, anterior to peak activation for words vs scramble (Fig. 2B). Contrasting words with faces shows no preferential recruitment anywhere in the left ventral visual stream. This result indicates that despite both faces and words being trained for a comparable amount of time, recruitment of the left ventral stream and the fusiform gyrus in particular was the same for both categories.

4.4. Analysis of behavioral tasks during fMRI session

When analyzing participants' behavioral results during fMRI visual

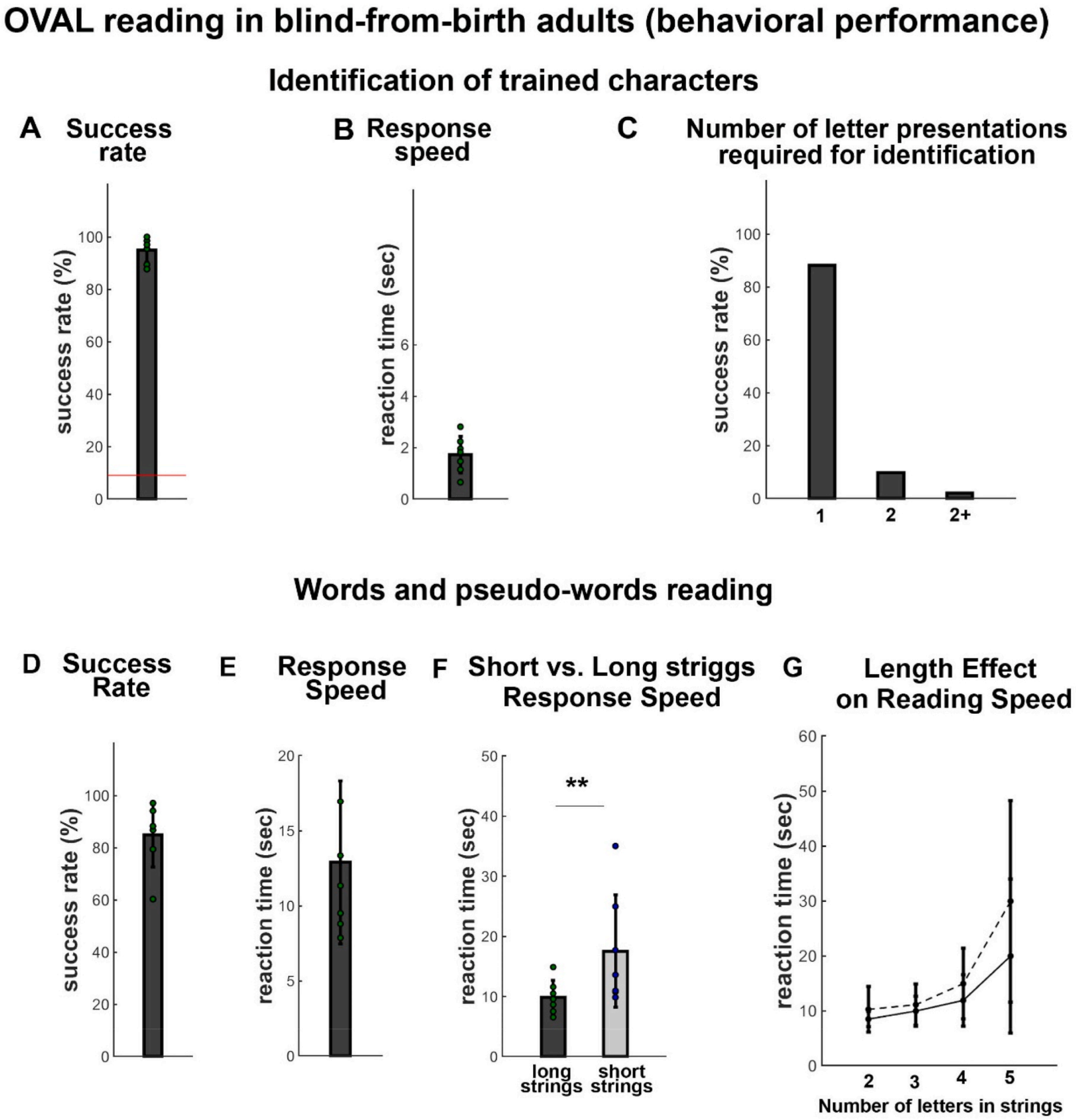


Fig. 3. OVAL reading in congenitally blind adults
OVAL letter identification - Congenitally blind adults (n = 7) achieved high letter identification accuracy rates following 6 h of OVAL training (A), as well as fast response speed (B). Most letters were correctly identified following one letter presentation (C). In addition to accurate letter identification, after 6 of training, blind participants were also accurate and fast in reading words of up to 5 characters (D, E), and showed longer latencies for longer than shorter strings (F). Length effect is evidenced in both words and pseudo-words (G). In all graphs, error bars represent standard deviations (SD). Asterisks represent statistically significant differences: **p < 0.005; *p < 0.05. Red lines represent chance level.

categories experiment following 12 h of OVAL training, we observed that participants were accurate in identifying all exemplars belonging to all categories above chance level. Specifically, participants correctly recognized words at 93.06%, (SD = ±8.19%, t (7) = 17.95, $p < 0.001$, $d = 7.33$), faces at 87.5% (±16.46%, t (7) = 8.11, $p < 0.001$, $d = 3.31$) and hands at 70.83% (±15.59%, t (7) = 5.94, $p < 0.001$, $d = 2.43$) (Fig. 1A).

4.5. Part III: OVAL reading in congenitally blind adults

4.5.1. Letter identification

At the completion of the basic 6-h OVAL training program, we tested our blind participants on a letter identification task. Results showed that all participants were able to identify letters, correctly identifying 95.0% (SD = ±4.65%) of the letters on average, significantly above chance level (9%) (t = 457.67, p < 0.00001). (Fig. 3A). In addition, when analyzing reaction times, it emerged that participants needed only one repetition of the letter on average to correctly identify it, with average reaction times of 1.73sec (±0.71%) (Fig. 3B).

4.5.2. Word/pseudo-word reading task

We assessed whether the letter identification capacity of our participants following this short reading-specific training extended to read new, untrained words and pseudo-words composed of the trained 11 OVAL letters. Experimental stimuli were not presented during training and were chosen at random from the entire possible Hebrew vocabulary (limiting the options to words containing only trained letters), thus chance level performance is close to zero. Blind individuals correctly read 84.87% of the words/pseudo-words on average (SD = ±12.21%). (Fig. 3D).

We entered the average accuracy rate for each participant into a repeated-measures ANOVA with stimulus-type (words; pseudo-words) and stimulus-length (short, i.e., 2–3 characters; long, i.e., 4–5 characters) as within-participants factors. This ANOVA revealed no effect of stimulus type or length on reading accuracy, with a trend towards words being read more correctly than pseudowords (F = 4.55, p = 0.07, η2p = 0.39). All other effects or interactions were non-significant (F < 2.92, p > 0.13).

When analyzing reaction times, we observed that readers identified an OVAL string after 12.48 s on average (about 3 word's repetitions; ±5.42 s) (Fig. 3E). We entered individual average reaction times into a repeated-measures ANOVA, with stimulus-type (words; pseudo-words) and stimulus-length (short, i.e., 2–3 characters; long, i.e., 4–5 characters) as within-participants factors. This ANOVA revealed that the main effect of stimulus-length was significant ([F = 13.02,p = 0.009, η2p = 0.65]) due to participants being faster in reading short than long words (short words: M = 11.06 s ± 4.19 s; long words: M = 19.86 s SD = ± 10.78 s) (Fig. 3F). No other effect or interaction was significant.

5. Discussion

In this work we aimed at characterizing for the first time the temporal dynamics characterizing the arising of computation-specific neural specialization in the deprived visual cortex when processing an atypical sensory input -in this case the neural specialization for a novel orthography, the OVAL, via the non-typical auditory modality in congenitally blind expert SSD users. We show modulation of neural activity in the right ventral visual stream following 2 h of novel auditory script learning. This modulation was observed only in an explicit OVAL letter identification task, and not while participants performed an implicit recognition of OVAL letters (via a color recognition task). Neither pseudo-letters or false-fonts with similar shape and color attributes did preferentially recruit the ventral visual stream following letter training. The lack of response to other visually-similar stimuli, including the same letter-stimuli during an orthogonal task of color recognition, stresses the involvement of the ventral visual stream in auditory character identification. Crucially, when blind adults were tested after ~12 h of OVAL training using a more complex reading task such as longer words and word combinations, we observed a more typical neural recruitment occurring in the left ventral visual stream only, in a region including the location of the left Visual Word Form Area (VWFA) as defined in the sighted brain. Our results thus suggest that after 2 h of training with a novel category of stimuli (i.e., letters conveyed via SSD belonging to a novel orthography) the deprived ventral visual stream is already recruited, albeit not in a fully specialized manner. In other words, these results suggest, in line with previous evidence (Striem-Amit et al., 2012) hat large-scale recruitment of the deprived ventral visual stream do occur very rapidly, already after 2 h of SSD training. However, computation-specific recruitment, in this case the typical laterality reported for letter identification (i.e., occurring in the left rather than in the right hemisphere) takes longer to arise. Importantly, our behavioral results prove that the OVAL orthography can be learned quickly, thus indicating and potentially promoting its suitability for reading rehabilitation in blind individuals.

5.1. Recruitment of the visual cortex for an auditory script

Following 2 h of a novel auditory-based script training, whole-brain analysis revealed rapid recruitment for auditory script processing in the right ventral visual stream. The deprived ventral visual stream has been repeatedly shown to be recruited for shape processing via the auditory modality (Amedi et al., 2007; Striem-Amit et al., 2012), yet this is the first study testing the dynamics of rapid plasticity to a new category of auditory-conveyed stimuli, i.e., after 2-h of dedicated training. While onw study from our group tested congenitally blind on word processing using Hebrew letters transformed via SSD to the auditory modality (Striem-Amit et al., 2012a),participants in those studies were only tested following longer formal training, in addition to non-quantifiable previous knowledge of letter shapes as part of cultural experience and non-formal training.

The current results confirm that despite the sound-discrimination properties of the letter identification task, 2-h dedicated training are already enough to allow participants to extract shape-related information embedded within the sounds to identify OVAL letters, as revealed by ventral-stream selective recruitment. This, in turn, strengthens the proposal that the main computational property of the ventral visual stream may be shapes' processing, independently of the sensory modality used as input (Heimler et al., 2015). In addition these results further expand previous findings indicating that 2-h training are already enough to allow large-scale division of labor between the ventral/dorsal stream in the congenitally blind brain (Striem-Amit et al., 2012).

These conclusions are in-line with the results of a study by Siuda-Krzywicka et al., investigating cortical reorganization following extensive tactile Braille training in sighted (Siuda-Krzywicka et al., 2016b). Specifically, this study traced cortical modulation in response to several months of tactile Braille training in sighted, and observed specific modulations of visual regions in response to shape and letter processing in the Fusiform Gyrus. Interestingly, these same stimuli did not trigger a modulated response in the primary somatosensory cortex, the primary modality for Braille reading. Nonetheless, another complementary study (Debowska et al., 2016) did report bilateral increased activity in the somatosensory cortex following extensive Braille instruction in sighted, though flanked by bilateral recruitment of the Fusiform Gyrus in response to the same Braille-conveyed stimuli. Unlike the study by Debowska et al. we did not observe any modulation in the auditory cortex following training, neither after rapid training nor after more extensive OVAL training. The lack of increased recruitment in the auditory cortex, which in the present case represents the sensory modality through which the OVAL stimuli are conveyed to our participants, could be explained by the fact that our participants received previous training in auditory object-recognition. While all our participants were already experts auditory SSD users, sighted participants from the study by Debowska et al. were naïve to tactile identification of shapes prior to the initiation of their study. It is possible that tactile training for sighted participants mainly increased tactile expertise, while in the case of our congenitally blind adults which were already proficient in auditory shape-recognition, training immediately tapped into computations related to shape processing rather than auditory tone analysis. Another notable difference between the present study and the study by Debrowska et al. is the difference in visual experience among the two experimental groups. The present study tested congenitally blind adults while the study by Debrowska et al. tested sighted adults. Although none of the described experiments used vision directly, underlying neural differences among these groups may account for the differential involvement of the direct sensory modality in both experiments. Future studies directly comparing congenitally blind and sighted on the same non-visual reading tasks, using comparable methodology and background experience are required to isolate the potential role of visual experience on the differential involvement of the sensory modality through which stimuli are conveyed. Future studies would also be able to use different fMRI paradigms, such as even-related designs, to differentiate neural recruitment in response to correct and incorrect trials, and test whether accuracy correlates with neural responses.

5.2. Rapid recruitment of the right ventral visual stream for a novel auditory script

Rapid recruitment for script processing was lateralized to the right ventral visual stream following 2 h of script acquisition. The right-lateralization of the presented results is surprising considering the typical lateralization of the reading network to the left hemisphere, and specifically to the left Visual Word Form Area within the Fusiform Gyrus (Cattinelli et al., 2013). What could explain the rapid right lateralization of script processing rather than the typical left VWFA recruitment? First, EEG studies following the developmental trajectory of left lateralized specialization to print show initial right lateralization of the N170 marker, the typical negative amplitude observed in electroencephalogram (EEG) when participants process written texts, with the following migration to the left hemisphere when reading becomes automatic (Maurer et al., 2005b). This result was observed both when studying children acquiring reading for the first time using the typical visual orthography of their spoken language, (Maurer et al., 2005; Maurer et al., 2005a), as well as in adults learning an artificial visual script representing their spoken language (Maurer et al., 2010). These results may suggest that this right N170 sensitivity to visual script emerging before reading becomes automatic may facilitate and possibly even drive the typical left-lateralized response observed in proficient adult readers (Bentin et al., 1999; Maurer et al., 2008; Maurer et al., 2005; Maurer et al., 2005a; Zhang et al., 1997). It is possible that the neural forces behind the right-lateralized recruitment of the ventral stream in our participants were similar to those driving the right lateralized N170 electrical activity observed in both children and sighted adults, during initial stages of script acquisition. In addition, similarly to the neurophysiological studies above, after longer training and exposure, preference to written words, here conveyed via the auditory modality, emerged in the typical location of the Visual Word Form Area in the left hemisphere. These results, in turn may mimic the migration of the N170 signal to the left hemisphere following more reading instruction in children following 2 years of schooling (Maurer et al., 2006). Another possibility explaining the right lateralized recruitment for OVAL script is that only broader computations, such as general object recognition properties processed in the ventral visual stream, can finalize rapidly following such short training. It has been shown that following 2 h of training on auditory object recognition, the broad division between the ventral visual stream for object recognition and the dorsal stream for location processing can emerge (Striem-Amit et al., 2012). Thus it remains possible that the short duration of training in the present study allowed only this general computation for object recognition to emerge, while the fine-tuned parcellation within the ventral visual stream and its lateralization for the processing of individual and specific object categories takes longer to develop. A third non mutually-exclusive possibility is that the initial emergence of orthographic processing in the right hemisphere originates from competition on representational space between reading and face processing. Studies on sighted individuals show that during the process of reading acquisition, activations for reading are established in the left hemisphere on the expense of initial bilateral activation for faces, which consequently becomes right-lateralized (Dehaene et al., 2010). In contrast to sighted individuals who are extensively exposed to faces from birth, congenitally blind adults in the present study learned to read during the appropriate window for reading acquisition in age 5–6, yet were not extensively exposed to faces during development. Thus, it could be that in the absence of underlying bilateral dominance for face processing due to lack of exposure to face-shapes during critical developmental periods, there was no underlying driving force for the initial left-lateralization for reading. In other words, it is possible that initial lateralization for reading could require the scaffolding of expertise with face processing. This possibility is strengthened by the observed specificity of the left VWFA for words processing over hands, following more prolonged training with OVAL reading. Instead, the current results showed that specificity of the left VWFA for words over faces was still lacking. Finally, another possibility relates to the possible interactions between melody and language/text representations. Indeed, unlike traditional visual scripts, OVAL creates melodic representations of letters' objects. It has been shown that while language is typically left lateralized, melody is predominantly right lateralized. A previous study that tested hemispheric lateralization for spoken syllables vs. melodic representation of visual letters through the vOICe SSD, found that unlike left lateralization observed in spoken syllables processing, the processing of visual letters converted to sound showed bilateral hemispheric processing in both sighted and blind (Proulx et al., 2020). In another study, this time comparing musicians and non-musicians, similar right-lateralization in response to pitch processing, compared with bilateral response to language, has been shown in music experts (Besson et al., 2007).

Due to the strict inclusion criteria, and the great time investment required from participants, the experimental cohort is limited. Although current trends in neuroscience shift away from case studies and small cohort designs, rare populations and studies requiring time-consuming tasks contribute greatly to theoretical and clinical neuroscience. One advantage of small cohort designs, is avoiding averaging across individual differences which may mask results (Furlan et al., 2018). Following the present work that establishes ventral stream recruitment to novel script acquisition in the rare population of congenitally blind, future studies should expand these results to broader populations, such as late and partially blind, which will enable the comparison of ventral stream plasticity and lateralization across different experimental cohorts.

Another limiting factor of the present study is that following more prolonged training, participants were tested on whole-words rather than letters. However, studies show left lateralized recruitment of the Fusiform Gyrus for text composed of both whole-words as well as individual letters (Flowers et al., 2004; Garrett et al., 2000; Pernet et al., 2005; Vinckier et al., 2007). Thus, this task-difference cannot fully explain the initial rapid right lateralization for text processing, followed by its emergence in the left hemisphere after more prolonged training.

5.3. Neural processes mediating new or artificial script in sighted adults

As all of the participants in the present study were Braille-literate, OVAL represents a second orthographic representation for participants' spoken language. Although there were no previous investigations into "artificial" script acquisition in blind individuals, several studies addressed the acquisition of a second orthography for a spoken language by sighted adults. These studies either used the typical sensory modality, vision, yet using an artificial orthography that is perceptually different from the native orthography (such as assigning Korean letters to English phonemes, or assigning face shapes or houses as graphs representing graphemes), or using the non-traditional tactile modality, i.e., using traditional Braille for naïve-to-Braille sighted adults. One hypothesis in these studies is that the increased tuning and specialization of the VWFA to the native orthographic representation would reduce its plasticity to the processing of a perceptually different orthography (Martin, Durisko et al., 2019). The introduction of an artificial orthography rather than the study of recruitment patterns for the acquisition of a second language and its orthography enables to disentangle orthographic acquisition from language acquisition. First, a study by Moore and colleagues (Moore et al., 2014) shows that the acquisition of an artificial orthography for English either by mapping foreign Korean letters (that are perceptually different from English letters) to English phonemes or by mapping images of faces to English letters, results in recruitment of the VWFA following several weeks of script acquisition. A comparable study, in which faces represented phonological units, either by mapping faces to graphemes, or faces to syllables, shows bilateral VWFA recruitment for the syllabic representation, and left-lateralized VWFA recruitment in the alphabetic representation (Hirshorn et al., 2016). Interestingly, no change in VWFA lateralization or strength of activation was observed in either case following additional training of several more weeks, indicating that after several weeks of training with a novel orthography, the properties of VWFA recruitment remain stable (Martin, Hirshorn et al., 2019). Together, these results indicate that a wide range of novel visual orthographies can recruit the VWFA, even when the novel scripts are acquired in adulthood (Martin, Durisko et al., 2019). Studies of sighted adults trained to read using a non-traditional modality, namely Braille, in which each letter is assigned a spatial tactile pattern similarly show that after several months of training, the left VWFA is recruited for reading tasks using the tactile modality as well (Debowska et al., 2016; Siuda-Krzywicka et al., 2016a). These latter results highlight that the left VWFA can be recruited in the sighted brain by novel scripts learned in adulthood even when such scripts are conveyed through a different sensory modality than the original modality used for reading (i.e., vision). In other words, these results suggest that plasticity in this region in the sighted brain is not limited to the transfer between representations within the same modality, but to representations across modalities as well. It is intriguing though that none but one of the above studies found right-hemisphere activation in response to the novel orthography (Hirshorn et al., 2016), following about 30 h of training. Notably however, none of the studies tested fMRI responses following early stages of script acquisition, after only 2 h of reading. It is possible that had these orthographies been tested at the very initial stages of orthographic acquisition, such as after 2 h similarly to the present study, they would had also observed a right lateralized ventral stream recruitment, possibly driven by basic perception of characters as objects. Other possibilities, as discussed above, are that the right lateralization reported here after short OVAL training reflect inherent differences between the sighted and blind “visual” brain and/or specific interactions between melody- and orthographic-related representations.

5.4. OVAL applicability for the study of the reading network in blindness, and reading rehabilitation for the blind

The behavioral results collected in our blind participants after more extensive OVAL training (i.e., after 6 h of training and again after ~12 h of OVAL training tested in the fMRI scan) together with the results showing the recruitment of the left VWFA area for OVAL reading after ~ 12 h of training carry two important implications. First, the success of OVAL acquisition in blind users shows its possible potential in reading rehabilitation in this population. The primary method for reading used by blind individuals today is the tactile Braille code. Yet due to the difficulty in mastering Braille, only a small percentage of the blind and visually impaired population uses it extensively (Scheithauer and Tiger, 2012). The present study, however, relied on a group of congenitally blind SSD experts. However, our previous results documenting OVAL ease of acquisition by sighted non-expert SSD users (Arbel et al., 2020), strengthen the conclusion that OVAL may be a suitable reading rehabilitation tool, perhaps even beyond the congenitally blind population. For instance, evidence suggest that Braille reading requires a great tactile sensitivity in order to successfully differentiate among Braille letters, contributing to extremely long and challenging training programs (Grant et al., 2000). Therefore the OVAL script may prove very useful for late-blind individuals who lack the tactile sensitivity needed to master Braille with an accessible reading method (Oshima et al., 2014). Yet some limitations for the feasibility of OVAL reading in the late blind population do exist. First, blind individuals face many challenges, and may be hesitant in investing time in learning to read via a non-traditional method. It could be that some individuals would still prefer text-to-voice converters over active reading, in order to save time. Second, unlike traditional Braille that can also be used in physical books, OVAL uses electronic equipment, and thus currently cannot provide the classic experience of holding and skimming through a regular book -but future developments of the application may allow it. Future studies can further explore the attitude towards OVAL in late blindness, as well as the possible differences in cortical recruitment for OVAL reading in blind participants that have previous experience with SSD compared with participants who only learned reading via SSD.

A second important implication of the present study is that the OVAL script can be a useful tool for the study of reading acquisition as well as the reading system in the blind. While behavioral processes of reading acquisition and the neural networks mediating it had been studied extensively in the sighted population both during childhood (Dehaene-Lambertz et al., 2018) and adulthood (Dehaene et al., 2010), relatively little is known about these processes in the blind (Gillon and Young, 2002). The ease of OVAL acquisition in adulthood makes it a suitable research tool for the study of basic processes of reading and its acquisition in this population as well as the interconnections between the reading network and the visual, auditory and lingual networks that are known to be affected by reading in the sighted (Dehaene et al., 2010), yet lack parallel investigations in the blind. Moreover, OVAL can serve as an orthography learned both by blind and sighted to directly compare reading learning processes and mechanisms as well as plasticity mechanisms related to reading in both groups. Up until now the difficulty in acquiring Braille by sighted individuals and the inability to read visually by blind individuals resulted in the indirect comparisons between these two populations via different reading modalities and systems. Our results presenting OVAL’s ease of reading in sighted (Arbel et al., 2020) as well as in blind (Fig. 2) suggest that both groups can easily learn OVAL and participate in the same tasks using the same reading system. This can help to disentangle properties related to reading itself, from processes related to the experience with the specific sensory modality used as input. Notably, while a direct comparison between OVAL and tactile Braille in the current experimental cohort is suboptimal due to the vast experience our participants have with Braille, comparing OVAL reading with tactile Braille reading can implicitly be done by turning to the available literature. In papers describing the time scale of Braille acquisition in both sighted and blind it shows that 10 h of Braille reading is not enough to reach even the simplest task of letter recognition, due to the tactile difficulty (Debowska et al., 2016; Kauffman et al., 2002; Millar, 1977).

In conclusion, in the present study we show the ease of learning OVAL, an auditory script for reading, by a group of congenitally blind adults. We show that rapid recruitment for OVAL processing following only 2 h of reading instruction occur in the right ventral visual stream rather than the auditory cortex despite that learning of OVAL requires the interpretation of, and differentiation among auditory sounds. Finally, we show that although initial processing of OVAL is in the right ventral visual stream, following more prolonged training of ~12 h, OVAL reading recruits the typical left VWFA, establishing its typical neural processing as an orthography.

Credit author statement

RA and AM conceived the experiments. RA acquired the data. RA and BH analysed the data. RA, BH and AM wrote the paper. All authors reviewed the manuscript.

Data availability

Data will be made available on request.

Acknowledgements

This work was supported by an ERC Consolidator grant (773121 NovelExperiSense), an ERC POC grant (101123434 TouchingSpace360), and a European Union Horizon 2020 research and innovation program grant (101017884 GuestXR) (To AA). We thank all our blind participants for the time they invested in this work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108685.

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