Contents lists available at ScienceDirect





journal homepage: http://www.elsevier.com/locate/dcn



Word and object recognition during reading acquisition: MEG evidence



Sendy Caffarra^{a,*}, Clara D. Martin^{a,b}, Mikel Lizarazu^a, Marie Lallier^a, Asier Zarraga^a, Nicola Molinaro^{a,b}, Manuel Carreiras^{a,b}

^a BCBL, Basque Center on Cognition, Brain and Language, Mikeletegi 69, Donostia 20009, Spain ^b Ikerbasque, Basque Foundation for Science, Maria Diaz de Haro 3, Bilbao 48013, Spain

ARTICLE INFO

Article history: Received 30 June 2016 Received in revised form 28 November 2016 Accepted 4 January 2017 Available online 10 January 2017

Keywords: MEG Reading acquisition Visual word recognition Speech processing Object recognition

ABSTRACT

Studies on adults suggest that reading-induced brain changes might not be limited to linguistic processes. It is still unclear whether these results can be generalized to reading development. The present study shows to which extent neural responses to verbal and nonverbal stimuli are reorganized while children learn to read. MEG data of thirty Basque children (4–8y) were collected while they were presented with written words, spoken words and visual objects. The evoked fields elicited by the experimental stimuli were compared to their scrambled counterparts. Visual words elicited left posterior (200–300 ms) and temporal activations (400–800 ms). The size of these effects increased as reading performance improved, suggesting a reorganization of children's visual word responses. Spoken words elicited greater left temporal responses relative to scrambles (300–700 ms). No evidence for the influence of reading expertise was observed. Brain responses to objects were greater than to scrambles in bilateral posterior regions (200–500 ms). There was a greater left hemisphere involvement as reading errors decreased, suggesting a strengthened verbal decoding of visual configurations with reading acquisition. The present results reveal that learning to read not only influences written word processing, but also affects visual object recognition, suggesting a non-language specific impact of reading on children's neural mechanisms.

© 2017 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Literacy is a relatively recent human invention that implies structural brain changes and a wide reorganization of different brain functions (Carreiras et al., 2009; Dehaene, 2011; Dehaene et al., 2015). It requires the acquisition of new linguistic abilities (e.g., letter-sound association, linguistic decoding of visual configurations), as well as the refinement of nonverbal visual skills (e.g., fine-grained visual object recognition). However, it is still unclear how these linguistic and non-linguistic changes can support reading acquisition and what is their relative contribution during reading development. Recent theoretical models assume that during the first stages of reading development new audiovisual objects need to be created and stored. Hence, changes in phonological processing are considered a primary requirement to reliably learn and memorize new visual objects (i.e, letters and words; Blomert, 2011). On the other hand, a different theoreti-

* Corresponding author at: BCBL, Basque Center on Cognition, Brain and Language, Paseo Mikeletegi 69, 20009 Donostia-San Sebastian, Spain. *E-mail address:* s.caffarra@bcbl.eu (S. Caffarra). cal perspective mainly emphasizes the specific role of the visual domain and describes reading acquisition as a visual perceptual learning, which requires an early reorganization of the brain's ventral stream (Dehaene et al., 2015; Kolinsky et al., 2011; Reis et al., 2006; Ventura et al., 2013). Unfortunately, most of the evidence so far collected on this topic comes from studies in adult participants. These findings cannot be easily generalized to children learning to read and they cannot directly inform us about the developmental trajectories of different reading-related brain changes during reading acquisition in childhood.

The present MEG study will specifically investigate verbal and nonverbal changes while children learn to read. Specifically, the aim of the experiment is twofold: 1) providing a temporal and spatial description of how reading acquisition affects children's linguistic mechanisms in the auditory and visual modality; 2) testing whether and how children's visual object recognition is affected by learning to read.

Most of what we know about brain areas involved in reading processing comes from studies on adults (Bolger et al., 2005; Jobard et al., 2003), which showed that written words activate the left language network in skilled readers (Dehaene et al., 2010;

http://dx.doi.org/10.1016/j.dcn.2017.01.002

^{1878-9293/© 2017} The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4. 0/).

Dehaene, 2011; Simos et al., 1998). When literates were presented with visual verbal stimuli, greater activations in the left occipitotemporal sulcus (visual word form area, Dehaene et al., 2010; Pinel et al., 2015) and in left frontotemporal regions (Carreiras et al., 2009; Dehaene et al., 2010) were observed compared to illiterates or less skilled readers. Modular models assume that the visual word form area is responsible for orthographic encoding at a first reading stage (McCandliss et al., 2003), while the left frontotemporal activity would reflect later processes of phonological, lexical and semantic encoding (Blomert, 2011; Jobard et al., 2003; Salmelin et al., 2000). Interactive models claim that frontal brain areas can influence the activity of the visual word form area even at early stages of reading. In this case the visual word form area is considered a multimodal integration hub, which receives topdown modulations from more anterior areas (Price and Devlin, 2011; for a discussion on different models of word recognition see Carreiras et al., 2014). Magnetoencephalographic (MEG) and electroencephalographic (EEG) data provided a contrastive pattern of results, with some studies showing brain responses in left occipitotemporal areas between 100 and 300 ms after stimulus onset (Bentin et al., 1999; Cohen et al., 2000; Helenius et al., 1999; Simos et al., 1998) followed by left temporal activity approximately 200 ms after stimulus onset (Carreiras et al., 2015; Simos et al., 1998, 1999; for a review see Salmelin et al., 2000), and some others showing frontal activations even before 200 ms (Cornelissen et al., 2009; Woodhead et al., 2014). Those two brain responses (i.e., frontotemporal and occipitotemporal) increase as reading performance improves (Dehaene et al., 2010; Pegado et al., 2014; Pinel et al., 2015) and quick reading-induced changes can be observed even after few training sessions (Hashimoto and Sakai, 2004; Song et al., 2010; Yoncheva et al., 2010; Xue et al., 2006).

Studies on children's reading acquisition also suggest a quick reorganization of brain networks. However, different results have been reported depending on the paradigm and the amount of reading instruction examined (see Table 1). Neuroimaging studies using longitudinal and cross-sectional designs showed changes in left occipitotemporal areas (Ben-Shachar et al., 2011; Brem et al., 2010; Pugh et al., 2013). Cross-sectional studies also showed changes in frontotemporal areas (Pugh et al., 2013; Turkeltaub et al., 2003), whose localizations were highly similar to those of adults (Houdé et al., 2010; Martin et al., 2015). Variations in occipitotemporal activity were observed after few training sessions (Brem et al., 2010), with an increased engagement of posterior occipitotemporal areas as reading performance improves (Shaywitz et al., 2002; for a metanalysis see Martin et al., 2015). Modulations in left frontotemporal responses were mainly observed in cross-sectional studies that considered a wider period of formal instruction (Pugh et al., 2013; Turkeltaub et al., 2003). Few electrophysiological studies are so far available and they mainly focused on short periods of reading instruction (from few hours to one year). They adopted a longitudinal design and reported changes in occipital brain responses with reading training (Brem et al., 2010; Maurer et al., 2006). These brain responses appeared later in time as compared to adults (later than 200 ms after stimulus onset, Maurer et al., 2006; see also Maurer et al., 2005) and were more bilaterally distributed (Brem et al., 2010; Maurer et al., 2006).

The present MEG study will examine a group of children who received different amounts of reading instruction (up to two years) in order to test whether and when occipital and temporal brain activity changes can be observed in developmental reading processes.

Literacy does not seem to induce changes only in processing of written verbal material, but also in speech processing. Neuroimaging studies on adult readers showed that auditory verbal stimuli usually elicit greater left parieto-temporal activity (i.e., planum temporale) relative to illiterates, especially when the task involves repetition or lexical decision (Castro-Caldas et al., 1998; Dehaene et al., 2010; Dehaene, 2011). These areas are supposed to be involved in grapheme-phoneme conversion (Blomert, 2011; Dehaene, 2011) and their activation would increase because the link between phonemic and graphemic representations is strengthened as reading improves (Dehaene et al., 2015; Pattamadilok et al., 2010). Electrophysiological studies provided a temporal characterization of these brain activation changes, showing left temporal sensitivity to spoken words 300 ms after stimulus onset (Helenius et al., 2009; Simos et al., 1998, 1999), which depends on reading performance (Helenius et al., 2009).

Data on literacy and children's speech processing are scarcer and mainly focused on reading disorders. Similarly to adults, skilled young readers listening to speech usually exhibit increased left temporal activations compared to reading-impaired children (Blau et al., 2010; Monzalvo et al., 2012; but see Simos et al., 2000), and these responses correlate with children's reading skills (Monzalvo et al., 2012). Very few studies on speech-related changes during normal reading development have been carried out. In Pugh et al. (2013) a group of children with different degrees of reading performance (5-9 years of age) had to decide whether a picture matched with the following spoken stimulus (a word or a pseudoword). Positive correlations were found between behavioral reading scores and brain responses to spoken targets in the left frontotemporal cortex and precuneus. In Monzalvo and Dehaene-Lambertz (2013) children with different amounts of reading instruction (6-9 years of age) passively listened to spoken sentences in native and foreign language. After few months of reading training, six-year-old children already showed increased activity for the 'native-foreign' contrast in left perisylvian regions. However, there was no difference between nine and six-year-olds in the 'native-foreign' comparison. Also, the overall brain responses to speech (native and foreign sentences) increased with age (similarly to Pugh et al., 2013). Unfortunately, the time sequence of these brain changes is still unclear since no electrophysiological study has so far investigated auditory processing as reading develops.

The present MEG study will provide for the first time a temporal description of reading-induced brain changes in children's speech processing.

Finally, recent findings suggest that effects of reading acquisition would extend beyond the verbal domain (Dehaene et al., 2010, 2015; Dundas et al., 2013; Pegado et al., 2014), influencing visual object processing (Reis et al., 2006). Behavioral studies showed that illiterate adults are usually less accurate than matched literate controls at detecting, recognizing, and naming visual objects (Ardilla et al., 1989; Kolinsky et al., 2011; Kremin et al., 1991; Reis et al., 1994; Szwed et al., 2012; Ventura et al., 2013). These differences are not specific to any object category and they would be the result of formal reading instruction, which represents an intensive perceptual training in detecting, segmenting, recognizing and interpreting visual representations (e.g., letter strings; Kolinsky et al., 1990; Reis et al., 2006). Neuroimaging studies on adults are only partially in line with these behavioral findings. Literate adults show increased occipital responses to visual stimuli compared to illiterates, suggesting an impact of literacy at early automatic stages of visual processing (Dehaene et al., 2015). However, when brain areas specifically associated to visual object recognition were considered (posterior-lateral sides of the fusiform gyrus, Malach et al., 1995) literacy showed a modest impact, with no changes in the peak responses to visual objects and small variations of the cortical boundaries for faces (Dehaene et al., 2010). Similarly, electrophysiological studies reported an enhancement of early posterior responses (140-180 ms) to different object categories (i.e., tools, houses, faces) as reading improves, however, later responses of object discrimination varied only for faces and houses (500 ms; Pegado et al., 2014).

Very few and heterogeneous data are so far available on the influence of reading acquisition in children's object recognition. Behavioral studies showed that children who can read better detect and segment visual objects compared to preschool children (Kolinsky et al., 1987, 1990). In contrast, fMRI (functional magnetic resonance imaging) and EEG studies that focused on a wide range of young participants showed that neural correlates of object recognition remained essentially constant across ages (Friedman et al., 1988, 1992; Golarai et al., 2007; Nishimura et al., 2009; Scherf et al., 2007). It should be noted that these studies never considered literacy as an experimental factor. Also, it has been claimed that object specific activation is particularly difficult to be mapped in young children (Aylward et al., 2005; Gathers et al., 2004; He et al., 2015). These mapping difficulties might be due to the high variability of brain response localizations across young participants (Gathers et al., 2004). However, the factors that account for this variability are still unclear.

The present MEG study will investigate for the first time the impact of reading acquisition on children's object recognition in order to test whether literacy can explain a certain amount of variations in children's brain responses to visual objects.

1.1. The present study

The present MEG study investigated the effect of reading acquisition on verbal processes (visual and auditory modality) and object recognition in a group of children with different ages and degrees of reading expertise.

Children's evoked related fields (ERF) in response to visual words, auditory words and visual objects were examined and compared to responses to their scrambled counterparts. We hypothesized that brain responses to the three types of stimuli should change relative to scrambles as reading develops. Also, a statistical comparison across tasks could inform about the relative contribution of verbal and nonverbal brain changes during reading development.

Written words should trigger the activation of the left language network through the left ventral cortex as reading expertise increases (Dehaene et al., 2010; Dehaene, 2011; Simos et al., 1998). Specifically, written words should elicit greater brain responses over left occipitotemporal sites (200–300 ms; Brem et al., 2010) and greater temporal activity (Carreiras et al., 2015; Salmelin et al., 2000). The magnitude of this effect should negatively correlate with the number of errors during reading.

Based on the previous literature, auditory words might elicit greater left temporal responses relative to scrambles (Dehaene et al., 2015; Monzalvo and Dehaene-Lambertz, 2013) approximately 300 ms after stimulus onset (Helenius et al., 2009). If the links between orthographic and phonological representations are strengthened by reading training, the magnitude of this effect should increase as reading performance improves.

Since literacy represents a strong perceptual training that leads to detect and interpret visual stimuli in a symbolic way (Hoving et al., 1974; Reis et al., 2006), reading performance should influence brain responses for object recognition relative to scrambles (especially in posterior regions; Dehaene et al., 2015).

Finally, comparing the impact of reading on auditory and visual tasks enables to estimate the relative weight of auditory and visual brain changes in reading acquisition. If phonological changes are the essential requirement to letter recognition (Blomert, 2011) the correlations between reading scores and auditory brain changes should be stronger than those regarding visual object responses.

This is the first MEG study testing the effects of reading acquisition on children's verbal and nonverbal mechanisms. It gives the possibility to confirm and complement what was observed so far in literate and illiterate adults. Also, it sheds new light on neural correlates of children's visual object recognition during reading acquisition.

2. Material and methods

2.1. Participants

Thirty-eight Basque-Spanish simultaneous bilingual children participated in the study (20 females, mean age: 6.4 years, SD: 1). Due to excessive movements or impossibility to attend to more than one experimental block, eight children were excluded from further analyses. The final sample of participants consisted of thirty Basque-Spanish bilingual children (11 females, mean age: 6.7 years, SD: 1, age range: 4-8; Basque AoA: 0; Spanish AoA: 1 year). All the participants lived in the Basque country, used Basque on a daily basis and followed a formal education in Basque since kindergarten. Formal reading instruction in Basque began around the age of six. However, some literacy experience could be present even before six years of age since kindergartens already provided games with letters and syllables. Note also that Basque has a transparent orthography that can be easily learned by young children. Based on parents' reports, all children were highly-proficient in spoken Basque and Spanish (on a scale of 1–10, the average was 8.3, SD: 1.6 for Basque, and 8.1., SD: 1.7 for Spanish), received different amounts of literacy education (from 0 to 18 months) and showed different levels of reading skills in Basque (on a scale of 1-10, the average was 5.0, SD: 3.8). None of the participants was repeating or had skipped a grade and their attendance to school was regular. All participants had normal or corrected-to-normal vision, normal hearing, no selfreported neurological disorders and no suspicion of developmental reading problems.

During a pre-test of reading skill assessment, all participants were presented with a list of 80 Basque words and 80 Basque pseudowords. Children showed a wide range of reading skills (average of errors during word reading: 46.1, SD: 64.3, range: 0-160). A picture naming task and the Raven's progressive matrices test (taken from Kaufman brief intelligence test, K-BIT, Spanish version, 2009) were used as measures of vocabulary size and nonverbal intelligence, respectively. The group of participants showed high variability in vocabulary size (mean: 30.1, SD: 5.5; range: 19-41) as well as in intelligence measures (mean: 21.5, SD: 5.9; range: 11-31). Correlational analyses were carried out on the overall group of children (see section 2.3). Additional analyses took into account data from poor (n = 14, 4 females, mean age: 6, SD: 1.1, age range: 4–8; Basque AoA: 0; Basque global proficiency: 8.4) and skilled readers (n = 16, 7 females, mean age: 7.1, SD: 0.6, age range: 6-8; Basque AoA: 0; Basque global proficiency: 8.4). These two groups were created by performing a median-split of the overall number of errors during reading words and pseudowords. Skilled readers and poor readers showed similar levels of proficiency for Basque speech production and comprehension, but they differed in their reading and writing skills. Age, vocabulary size and nonverbal intelligence measures were not equated across groups (see Section 2.3; Table 2).

2.2. Materials

One hundred eighty Basque words were selected and divided in three lists: 60 were presented as visual words, 60 as auditory words, and 60 as visual objects (see Fig. 1). All words were concrete Basque nouns acquired early in life, highly-frequent, highly-familiar, with similar lexical features across the three lists (see Table 3). The lists of nouns were presented in three different blocks together with a control condition (i.e., scrambled items).

In the visual word block, nouns were presented in black letters on a white background $(960 \times 720 \text{ pixel array})$. The control

Table 1

Summary of neuroimaging and electrophysiological studies on brain changes during normal reading acquisition. For each paper, we describe the technique, children's age range, the total duration of formal reading instruction examined (y: years; w: weeks), the experimental design, the main comparisons of interest, the increased brain activity reported as reading improves.

Paper	Technique	Age range (years)	Time range of reading instruction	Design	Comparison of interest	Increased brain responses
Ben-Shachar et al. (2011)	fMRI	7–12	4y	longitudinal/cross- sectional	words with four different visibility levels, and correlation between behavioral reading scores and brain sensitivity	left occipitotemporal cortex
Brem et al. (2010)	fMRI +ERP	6	8w	longitudinal	words vs. false fonts	bilateral occipitotemporal cortex (bilateral N1, 200–300 ms)
Maurer et al. (2006)	ERP	6-8	1.5y	longitudinal	words vs. symbols	bilateral N1 (150-250 ms)
Pugh et al. (2013)	fMRI	5–9	4y	cross-sectional	correlation between behavioral reading scores and brain activity to print (written words and pseudowords)	left temporal and occipitotemporal cortex
Turkeltaub et al. (2003)	fMRI	6–22	16y	cross-sectional	words vs. false fonts, and correlation between behavioral reading scores and mean-activity difference	left frontotemporal cortex

Table 2

Mean scores and ranges for poor readers and skilled readers (standard deviations are in parentheses). Vocabulary size was measured with a picture naming task, and Raven's progressive matrices were used as a measure of nonverbal intelligence. Reading performance was measured as the number of errors during words and pseudowords reading. Parents were asked to rate on a scale of 1–10 children's skills in written and spoken Basque.

	Poor readers (n = 14)		Skilled Readers (n = 16)		р
	Mean (SD)	Range	Mean (SD)	Range	
Age (months)	72.5(13.0)	55-101	86.4 (7.7)	74–100	<0.01
Non-verbal intelligence	17.6 (4.7)	19–36	24.9 (4.5)	25-41	< 0.001
Vocabulary size	27.7 (5.2)	11-26	32.2 (5.0)	15-31	< 0.05
Words reading (n° errors)	43.6 (37.9)	1-80	3.0 (2.1)	0-7	< 0.01
Pseudowords reading (n° errors)	46.6 (34.7)	10-80	4.5 (3.5)	0-11	< 0.001
Basque written comprehension (1–10)	2.6 (3.6)	0-9	7.0 (3.0)	0-10	< 0.01
Basque written production (1–10)	2.9 (3.5)	0-8	7.0 (2.6)	0-10	< 0.01
Basque speech comprehension (1–10)	8.5 (1.6)	6-10	8.5 (1.4)	6-10	n.s.
Basque speech production (1-10)	8 (2.2)	4-10	8.1 (1.4)	6-10	n.s.

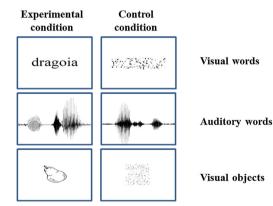


Table 3

General characteristics of the experimental materials. Each lexical feature did not differ across the three lists of stimuli (all *ps* > 0.05).

	Visual words	Auditory words	Object names
N° of letters	6.1 (1.3)	6.4 (1.2)	6.3 (1.1)
N° of syllables	3.1 (0.6)	3.1 (0.6)	3.2 (0.6)
Log-transformed frequency	1.0 (0.6)	0.9 (0.6)	0.9 (0.6)
AoA	1.6 (1.9)	2.0 (2.1)	2.0 (2.1)
Familiarity (0–10)	5.9 (0.7)	6.0 (0.8)	6.1 (0.6)
Imageability (0–10)	6.1 (0.4)	6.2 (0.4)	6.2 (0.4)
Concreteness (0-10)	5.8 (0.6)	5.7 (0.7)	5.9 (0.7)

Fig. 1. Examples of stimuli from the experimental and the control condition for each of the three blocks.

condition was created by breaking word images into little squares $(10 \times 10 \text{ pixel})$ and shuffling their spatial locations, so that the original written word was not recognizable anymore and each scrambled image was equiluminant with the original one (see Glezer et al., 2015 for a similar procedure).

In the auditory block, stimuli were presented in a male voice, and recorded at 44.1 Khz. The control condition was created by spectrally-inverting each word audio (i.e., the spectral content of the word signal was inverted around a center frequency of 2 kHz).

This spectral alteration made the inverted audio virtually unintelligible, but similar in intonation and spectral power to the original auditory word (Blesser, 1972; Obleser et al., 2007).

In the object block, 60 black-and-white line drawings of natural and man-made objects (selected from Sadat et al., 2014) were presented. Each image was scaled to fit within a 960×720 pixel array. The control condition was created by breaking object images into 10×10 pixel squares and randomly shuffling their locations. All pairs of regularly configured and scrambled objects were equated for luminance (see Grill-Spector et al., 1998; Vilberg and Davachi, 2013 for a similar procedure).

For each block, 12 items (6 regularly configured and 6 scrambled items) were randomly selected and presented twice in a row. These repeated trials represented the target items of a one-back task and were excluded from further analyses. Overall, each block contained

132 items each (60 regular configured items, 60 scrambled items, and 12 repetitions).

2.3. Procedure

Participants sat on a comfortable chair in a magnetically shielded room and were instructed to fixate the center of the screen (distance 150 cm). To make sure participants were attentive all along the experiment, the task consisted of pressing a response button whenever the current stimulus was identical to the previous one in the sequence (one-back task). Before each experimental block, participants received a short training block of 5 stimuli (with one repeated item) to make them familiarized with the task and the stimuli (visual words, auditory words and objects, depending on the current block). Auditory stimuli were presented between 70 and 80 dB through plastic tubes and silicon earpieces to participants' ears (average duration: 700 ms, SD: 95). Visual stimuli were presented at the center of the screen for 2000 ms with a visual angle of approximately 4°. The interstimulus interval was 1000 ms. Stimuli and block orders were randomized across participants. Every 20 items a short break was provided and longer pauses were given at the end of each block. Overall, the recording session lasted approximately one hour. Two participants were too sleepy to attend to the last experimental block (the object block in both cases).

2.4. Meg data recording and ERF analyses

Continuous cerebral activity was recorded (band-pass filter: 0.03-330 Hz; sampling rate: 1000 Hz) using the whole-scalp MEG system (Elekta-Neuromag, Helsinki, Finland) installed at the Basque Center on Cognition, Brain and Language. Each of the 102 sensors contained two planar gradiometers and one magnetometer. At the beginning of the experiment, the positions of four Head Position Indicator (HPI) coils were defined relative to the nasion and both preauricular anatomical points with an Isotrak 3-D digitizer (Fastrak Polhemus, USA). The head position was initially calculated relative to the coordinate system of the MEG helmet and continuously monitored during the recording session to register possible head movements. Eye movements were monitored with vertical and horizontal bipolar electrooculograms (VEOG and HEOG). Using MaxFilter (Ver. 2.2.12; Elekta-Neuromag), MEG data were individually corrected for head movements and subjected to noise reduction using the temporally extended signal space separation method (Taulu and Hari, 2009; Taulu and Kajola, 2005). Bad channels were substituted with interpolated values.

In order to obtain the event-related fields (ERFs) time-locked to experimental stimuli onset, the MEG data were subsequently analysed using Fieldtrip toolbox (Oostenveld et al., 2011) implemented in Matlab (Mathworks). Muscle artifacts expressed in the high frequencies (110-140 Hz) were automatically rejected. Average zvalues over sensors and time points in each trial were calculated and trials exceeding the threshold of a z-score equal to 25 were removed. Then, the recordings were low-pass filtered at 35 Hz and down-sampled off-line to 150 Hz. Heart beat and ocular artifacts were linearly subtracted from recordings using Independent Component Analysis (ICA) (Bell and Sejnowski, 1995). ICA components responsible for eye movements were identified calculating correlation values between the component signal and the activity of the VEOG/HEOG channels. Finally, MEG epochs were visually inspected to discard any remaining artifacts. Planar gradiometers were combined and event-related fields (ERFs) were obtained by averaging the remaining MEG epochs. A baseline correction was applied using an interval of -400 ms to 0 ms. On average, 63% (SD: 11) of trials were included after rejections. There were no significant differences in the number of accepted trials across conditions (F(1,7)=0.35, p=0.93) and across groups (F(1,27)=0.59; p=0.45).

To identify the cluster of sensors showing the greatest difference between regularly configured and scrambled conditions, we performed a nonparametric cluster-based random permutation test at the sensors level during the first second of stimulus presentation (Maris and Oostenveld, 2007). The analysis also enabled to identify the time windows where the difference between experimental conditions was maximized.¹ The averaged values of combined planar gradient entered the statistical analysis. This test increases the sensitivity of the statistics while controlling for multiple comparisons. First, for every sensor the experimental conditions were compared by means of dependent-samples t-tests. All contiguous sensors exceeding a preset threshold (p = 0.05) were grouped into clusters based on temporal, spatial and spectral adjacency. For each cluster the sum of the t-values was calculated and used at the clusterlevel statistics. Then, a null distribution assuming no difference between conditions was approximated by drawing 1000 random permutations of the observed data and calculating the maximum cluster-level summed t-values for each randomization. Finally, the observed cluster-level statistics were evaluated under the null distribution. When the clusters fell in the highest 5th percentile, we concluded that the data in the two conditions do not come from the same probability distributions; hence, they were significantly different.

For each participant and each time window of interest, the ERF difference between regularly configured and scrambled conditions was calculated at the sensors that were previously identified by the cluster-based random permutation test (and that showed a significant difference for at least 100 ms).

To estimate the degree of association between brain activity change and reading performance, partial correlations were computed between the effect size of each significant cluster (i.e., regularly configured condition minus scrambled condition) and the number of errors during word and pseudoword reading. All correlations were controlled for age, vocabulary size and nonverbal intelligence. Statistical comparisons between correlations of different tasks were carried out using cocor R package (Diedenhofen and Musch, 2015).

To further check for brain changes during reading development, we also looked at the brain responses of children whose reading performance was above and below the median (i.e., defined here as poor and skilled readers) and we performed additional clusterbased permutation tests on these two groups.

3. Results

Participants showed 87% of correct identification of repeated items (poor readers: 83%, SD: 5; skilled readers: 89%, SD: 4). Accuracy rates did not differ across blocks (F(2,87) < 2.03, p=0.14) and across groups (t(28) < 1, p=0.83). Results from correlation analyses are shown in Figs. 2, 4 and 6. Averaged ERF waveforms recorded during each block for poor and skilled readers are displayed in Figs. 3, 5 and 7.

3.1. Visual word block

Between 200 and 300 ms after stimulus onset, the overall group showed a greater activity for written words than scrambles over left posterior sites (p < 0.01). The magnitude of this effect (i.e., the brain activity difference between words and scrambles) negatively correlated with the number of errors made during reading (r = -0.45,

¹ These time windows were consistent with those reported in previous electrophysiological studies (visual words: Brem et al., 2010; Salmelin et al., 2000; auditory words: Helenius et al., 2009; Simos et al., 2000; visual objects: Friedman et al., 1988, 1992).

Visual Word 200-300ms Visual Word 400-800ms

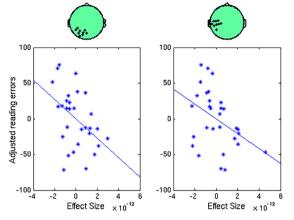


Fig. 2. Partial correlation between visual word responses and reading errors. Values from all participants (n = 30) are represented. The graphs show the residuals of number of errors in reading (y-axis) and the ERF amplitude difference (words minus scrambles) in the time windows of interest (left: 200–300 ms; right: 400–800 ms). Values were adjusted for age, vocabulary size, and nonverbal intelligence.

p < 0.01), after controlling for age, vocabulary size and nonverbal intelligence measures (see Fig. 2). Between 400 and 800 ms, words elicited greater responses than scrambles over left temporal sites (p < 0.01). Again, this effect size negatively correlated with the number of errors during reading (r = -0.41, p < 0.05, see Fig. 2). It is worth noting that the brain response changes observed in both time windows were specifically associated with reading expertise since the ERF effects did not correlate with participants' characteristics (i.e., age, vocabulary size, nonverbal intelligence) after correcting for reading performance (all ps > 0.05). Thus, brain responses to written words relative to scrambles progressively increased over left posterior (200–300 ms) and temporal sites (400–800 ms) as reading performance improved.

The analyses on poor and skilled readers showed results in line with the correlations above. Specifically, skilled readers showed stronger neural activity for words than scrambles over left posterior sites between 200 and 300 ms (p < 0.01) and a greater left temporal activity was observed after 400 ms (p < 0.01). Poor readers did not show any significant difference between visual words and scrambled words (200–300 ms: p = 0.22; 400–800 ms: p = 0.37, see Fig. 3). The between-group analyses on brain responses did not reach statistical significance (ps > 0.05).²

3.2. Auditory word block

Between 300 and 700 ms after stimulus onset spoken words elicited greater responses than scrambles over left temporal sites (p < 0.01). The magnitude of this effect (averaged word-scramble activity difference) did not correlate with the number of errors during reading (r = +0.11, p=0.29, see Fig. 4).³

Both poor and skilled readers showed greater left temporal responses for auditory words relative to scrambles (poor readers:

3.3. Visual object block

Between 200 and 500 ms after stimulus onset, visual objects elicited greater responses than scrambles over left sites (p < 0.01) and right posterior sites (p < 0.05). Partial correlations between the effect size (i.e., object-scramble activity difference) and reading performance were calculated for both groups of sensors. While the magnitude of the effect over left sensors negatively correlated with the number of reading errors (r = -0.31, p < 0.05), the rightlateralized brain responses did not show any significant correlation with reading measures (r = -0.05, p = 0.40, see Fig. 6).⁵ The left brain response changes did not correlate with age and nonverbal intelligence after correcting for reading performance (all ps > 0.05) but they still correlated with vocabulary size (i.e., scores from a picture naming task; r = -0.40, p < 0.05). Thus, greater left lateralized brain responses to objects versus scrambles were associated with improvements in reading and in verbal decoding of visual configurations (i.e., black-and-white pictures).

In skilled readers, the cluster-based permutation test revealed a significant difference between objects and scrambles in left posterior sensors (p < 0.05), with greater amplitudes for visual objects. A significant difference was observed for poor readers over right temporal sensors (p < 0.01, see Fig. 7). Between-group comparisons were not significant (p > 0.05).⁶

3.4. Comparisons across tasks

Statistical comparisons among the three tasks showed that the correlation between reading errors and brain responses to visual words did not differ in strength from the correlation of visual object effects (zs < 0.80, ps > 0.20; Pearson and Filon, 1898). This suggests that children's reading expertise had a similar impact on brain responses to visual words and objects. On the other hand, the correlation between reading errors and auditory brain changes was significantly weaker as compared to the correlations of visual objects and words (zs > 1.55, $ps \le 0.05$; Pearson and Filon, 1898).

4. Discussion

The present MEG study investigated children's verbal and nonverbal processes during reading acquisition. The results showed a wide reorganization of brain activity when verbal stimuli were visually presented, while no consistent variations were found in the auditory domain. Neural correlates of visual object recognition also changed as reading improved, suggesting that learning to read can influence how children treat visual representations.

The present results on written words confirmed that as reading skills improve, an increased left occipitotemporal activity can be seen around 200 ms (as similarly observed in longitudinal studies with children: Brem et al., 2010; Maurer et al., 2006). The distribution and the time course of this effect are compatible with those of the visual word form area, which is supposed to be the gateway region for reading that enables the access to abstract representations of letters (McCandliss et al., 2003), or a multimodal integration

 $^{^2}$ Two subsets of poor and skilled readers (n = 10), who were matched for age, vocabulary size and nonverbal intelligence, were also considered and further analysed. The results were similar to those presented above, with significant differences between words and scrambles only for the skilled readers. In addition, between-group comparisons revealed greater effects for skilled readers as compared to matched poor readers between 400 and 800 ms.

³ Scrambled audios elicited greater responses than spoken words within the first 200 ms after stimulus onset (p < 0.01). The effect size did not correlate with reading performance (r = -0.03, p = 0.45).

p<0.01, skilled readers: p<0.05, see Fig. 5). Between-group comparisons were not significant (p>0.05).⁴

⁴ Similar results were found for poor and skilled readers (n = 10) matched for age, vocabulary size and nonverbal intelligence.

⁵ Scrambles elicited greater responses than objects within the first 200 ms after stimulus onset (poor readers: p < 0.01; skilled readers: p < 0.05). The effect size did not correlate with reading performance (r = +0.08, p = 0.35).

⁶ Similar results were found for a subset of poor and skilled readers matched for age, vocabulary size and nonverbal intelligence (n = 10).

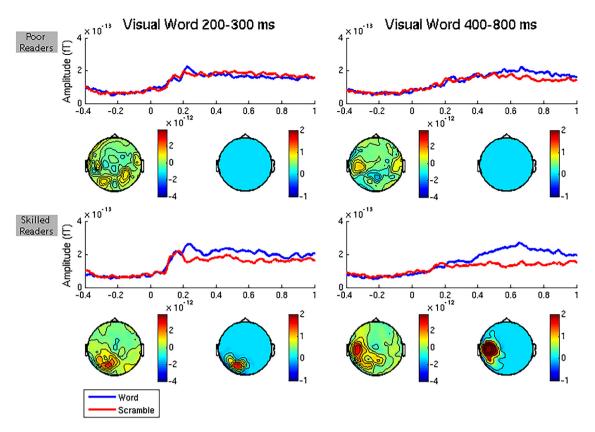


Fig. 3. Average ERF waveforms to visual words and scrambled words for poor readers (top) and skilled readers (bottom). The ERF responses were calculated averaging left posterior and left temporal planar gradiometers that showed significant ERF differences in the 200–300 and 400–800 ms intervals. Evoked responses to the scrambled words were subtracted from the responses to the visual words. For each time window of interest (200–300 ms; 400–800 ms after stimulus onset), topographic distribution of grand-average difference waveforms and *t*-values of the significant group of sensors are displayed below the ERF responses (on the left and right side, respectively).

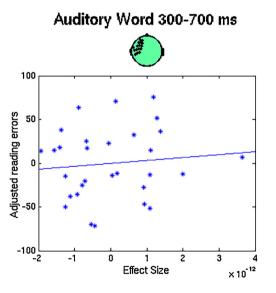


Fig. 4. Partial correlation between auditory word responses and reading errors. Values from all participants (n = 30) are represented. The graph shows the correlation between the number of errors in reading (residuals, y-axis) and the ERF amplitude difference (words minus scrambles) in the time window of interest (300–700 ms) after adjusting for age, vocabulary size, and nonverbal intelligence.

hub (Carreiras et al., 2014; Price and Devlin, 2011). However, since no frontal brain changes were found at this early stage of reading the current data do not provide evidence supporting interactive models (Price and Devlin, 2011).

Our findings on written words further reveal that when a long training period is considered (up to two years) children show a strong reorganization of brain responses, with an additional increase of left-lateralized brain responses at a later stage of processing (400-800 ms). According to modular models, this effect is supposed to reflect phonological, lexical, and semantic processes that would take place after a first stage of orthographic encoding (Pugh et al., 2013; Turkeltaub et al., 2003; Simos et al., 2000). Overall, the present MEG findings are consistent with what has been reported in cross-sectional studies using different techniques and experimental paradigms (Carreiras et al., 2009; Dehaene et al., 2010; Pugh et al., 2013; Turkeltaub et al., 2003). The time windows of interest are slightly delayed with respect to the adults (Salmelin et al., 2000), suggesting that reading mechanisms might be further automatized and speeded up through life (Maurer et al., 2005, 2006). Although previous studies suggest that occipitotemporal responses to visual words are bilaterally distributed after few reading sessions (Brem et al., 2010), the present findings reveal that an adult-like left lateralization of posterior responses can emerge within the first two years of formal reading instruction. The lack of between-subject differences together with the correlation values might suggest that the effect of reading acquisition on neural responses is continuous rather than a sudden change (see also Monzalvo and Dehaene-Lambertz. 2013).

Auditory words elicited greater responses relative to scrambles over left temporal sites 300 ms after stimulus onset. The distribution and time course of this effect are consistent with what previously reported, reflecting lexical and semantic access of spoken words (Helenius et al., 2009; Simos et al., 1998, 1999, 2000). However, this effect did not modulate as a function of reading performance, suggesting that reading acquisition did not strongly

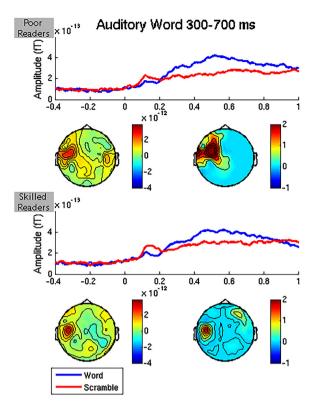


Fig. 5. Average ERF waveforms to auditory words and scrambled words for poor readers (top) and skilled readers (bottom). The ERF responses were calculated averaging left temporal planar gradiometers (which showed significant ERF differences between 300 and 700 ms). The evoked responses to the auditory scrambles were subtracted from the responses to the spoken words in the time window of interest. Topographic distribution of grand-average difference waveforms and *t*-values of the significant group of sensors are displayed below the ERF responses (on the left and right side, respectively).

change the way children processed auditory words relative to scrambles within the first years of formal instruction.⁷ The present findings are difficult to reconcile with previous neuroimaging data, which rather suggest an impact of literacy on auditory processes (Castro-Caldas et al., 1998; Dehaene et al., 2010; Dehaene, 2011; Helenius et al., 2009; Pugh et al., 2013).

Methodological differences across studies can contribute to explain these different patterns of results. Neuroimaging studies on adults highlight the strong impact of literacy on spoken word responses when people perform explicit tasks (e.g., rhyming, repetition, lexical decision tasks; Castro-Caldas et al., 1998; Dehaene et al., 2010; Dehaene, 2011). Importantly, they did not report brain changes during passive listening (Dehaene et al., 2010). Similarly, a neuroimaging study where children were passively listening to sentences did not systematically report reading-induced changes (Monzalvo and Dehaene-Lambertz, 2013). Variations in neural correlates of spoken sentences relative to foreign sentences were reported after few months of reading instructions (6 years old), but not after years (6-9 years old; Monzalvo and Dehaene-Lambertz, 2013; see also Simos et al., 2000 for a similar null effect). Apart from the task, the contrast of interest might also contribute to explain the different patterns of results. In Monzalvo and Dehaene-Lambertz (2013) significant differences in the speech network were observed between 6 and 9 years of age only when responses to native and foreign sentences were grouped, but not when they were compared against each other. Similarly, Pugh et al. (2013) reported an

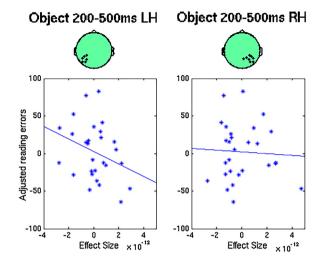


Fig. 6. Partial correlation between visual object responses and reading errors. Values from all participants (n = 28) are represented. The graphs show the residuals of reading errors (y-axis) vs. the ERF amplitude difference (objects minus scrambles) in the time window of interest (200–500 ms). Values were adjusted for age, vocabulary size, and nonverbal intelligence.

enhancement of left temporal responses after combining activity from words and pseudowords (Pugh et al., 2013). However, results concerning the direct contrast between words and pseudowords were not reported.

Altogether, these findings show that the impact of reading acquisition on the left spoken language network is evident only under specific experimental circumstances. Both the task and the contrast of interest might influence the final pattern of results (Dehaene et al., 2010; Monzalvo and Dehaene-Lambertz, 2013; Pugh et al., 2013). Given the paucity of studies on literacy and reading development it is difficult to draw definitive conclusions on this issue. Based on the available findings, we can claim that reading expertise does not have strong effects on auditory processes involved in passive listening. This questions a consistent automatic access to orthography during auditory word processing (Perre et al., 2011) and highlights that, at least in children, orthographic representations are not always activated by the passive listening to the corresponding words. In addition, reading acquisition does not seem to affect processes that are specifically related to the analysis of meaningful words and sentences compared to other auditory controls (i.e., scrambles, foreign sentences). Other auditory subdomains might be more affected by the experience of reading. Behavioural and electrophysiological studies seem to suggest that the processing of prosodic contours (Goswami et al., 2009; Molinaro et al., 2016), syllabic boundaries (Hornickel et al., 2009; Lizarazu et al., 2015; Morais et al., 1986) and phonological cues (Morais et al., 1979; Morais et al., 2007; Woodruff et al., 2014; for a review see Huettig and Mishra, 2014) might be more affected by reading expertise as compared to lexical analysis.

Brain responses to visual objects differ from those to scrambles over posterior sites (200–500 ms). The distribution and the timing of this effect are consistent with those reported in previous electrophysiological studies for recognition and semantic encoding of visual objects (Friedman et al., 1988, 1992; He et al., 2015). Importantly, we observed changes of these responses as a function of reading scores and picture naming scores, with increased left responses to objects relative to scrambles as reading and verbal decoding of visual images improves. The lack of clear differences between poor and skilled readers in the between-group comparisons might suggest that these brain changes gradually happen over time.

⁷ Note that the presence of a clear effect in poor readers confirmed that we had enough statistical power to detect differences even in this group of children.

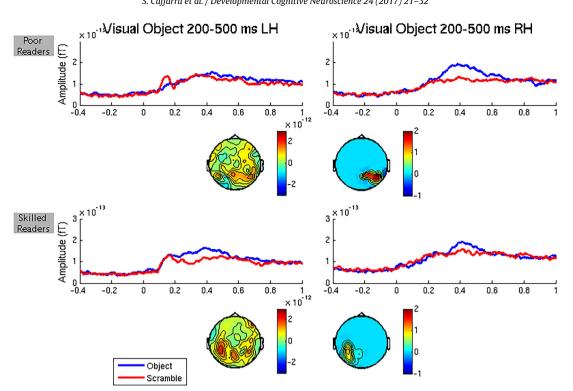


Fig. 7. Average ERF waveforms to visual objects and scrambled objects for poor readers (top) and skilled readers (bottom). The ERF responses were calculated by averaging left and right posterior planar gradiometers. Between 200 and 500 ms after stimulus onset the evoked responses to the scrambled objects were subtracted from the responses to the visual objects. Topographic distribution of grand-average difference waveforms and t-values of the significant clusters are displayed below the ERF responses (on the left and right side, respectively).

These findings show for the first time that neural correlates of children's object recognition change as they become more expert readers. Reading acquisition is associated with the activation of the left language network during children's object recognition. One possible explanation of the present finding is related to the linguistic decoding of visual material. This effect can be interpreted as reflecting a more efficient access to lexical codes through visual configurations after reading acquisition. As children learn to read they get trained to associate symbolic visual material (e.g. letters) with phonological, lexical and semantic content (Kolinsky et al., 1990; Reis et al., 2006). This training would influence the interaction between the visual and the language systems (for a similar proposal see Hoving et al., 1974; Reis et al., 2006) and it would enable the left language network to be activated by different types of visual representations.

The present findings can be alternatively explained by a progressive enhancement of the neural visual system while children learn to read. In this case, the present changes in brain responses to visual objects would be mainly due to a specific improvement of basic perceptual skills as the result of reading training. However, previously reported reading-related brain changes in primary visual areas were typically observed in earlier time windows (e.g., 100–200 ms; Pegado et al., 2014) and they were usually bilaterally distributed (Dehaene et al., 2010, 2015).

The greater involvement of the left hemisphere between 200 and 500 ms during object recognition seems to be more likely related to a stronger linguistic decoding of visual stimuli. This interpretation is further supported by the presence of a negative correlation between the left posterior brain responses to visual objects and children's ability to access linguistic codes given simple line drawings. The more children were able to verbalize schematic visual representations, the stronger the effect over left posterior sites.

Consistently with these findings, behavioral studies showed that literates are better than illiterates at naming pictures and retrieving linguistic information based on visual representations of objects (Ardilla et al., 1989; Kremin et al., 1991; Manly et al., 1999; Reis et al., 1994, 2001). Interestingly, literates' and illiterates' performances during picture naming are different especially when the visual configurations are two dimensional, contour based, and black and white (Reis et al., 1994, 2001, 2006). This suggests that the more the visual material implies a certain level of abstraction and symbolic representation (as in the case of letter strings), the stronger the effect of literacy on object recognition. Since reading represents a training in accessing linguistic information based on conventional visual representations, acquiring a new writing system would generally entrench the verbal decoding of graphic material. The effects of this training would not be restricted to letter strings but they could be generalized to those visual configurations that require a certain level of symbolism and conventional meaning (e.g., line drawings). This might explain why previous neuroimaging studies did not find strong brain changes with photographs and tridimensional representations (Dehaene et al., 2010; Pegado et al., 2014; see Reis et al., 1994 for similar null effects at the behavioral level).

The present findings enable us to reconcile previous contrasting and challenging findings reported in object recognition literature. For instance, reading expertise can help to explain why object detection areas are highly heterogeneous and particularly difficult to be mapped in children (Gathers et al., 2004). Similarly, the different patterns of response lateralization so far reported in visual object detection (i.e., left-lateralized, Sergent et al., 1992; Dawson et al., 2002) might be accounted by differences in participants' reading skills.

Moreover, our findings on visual objects seem to be in line with recent data on visual categorization (Franklin et al., 2008). In a visual-half field study on color categorization, a stronger involvement of left hemisphere was reported in adult readers compared to infants (Franklin et al., 2008). Although further investigations are needed in order to better define the exact role of literacy on visual analysis, this might suggest that reading acquisition has an effect not only on the way people decode figurative representations but also on the way they discriminate and categorize visual input.

Finally, the comparison between correlations of different cognitive domains showed that children's brain responses to visual configurations (i.e., words and objects) are more related to reading performance as compared to auditory brain changes. This suggests that during the first two years of formal education, reading has a stronger impact on the visual domain as compared to the auditory domain (Dehaene et al., 2010, 2015). The present result does not seem to support theoretical models that assume the presence of phonological changes before being able to observe any visual improvement (Blomert, 2011). Reading-related phonological brain changes might be more evident later on or might involve specific auditory subprocesses that were not examined in the present study (such as phonological awareness, Castles and Coltheart, 2004). Additional investigation is needed in order to draw definitive conclusions on this issue.

4.1. Limitations

The current study, as many electrophysiological studies on young participants, has several limitations. Due to low quality of data we had to exclude eight children from our analyses and two of the children included in the experimental sample could not attend to the last experimental block of the MEG recording session. In addition, it should be noted that children who achieved high reading performances were also those who received a substantial amount of formal reading instruction. Thus the effect of schooling and reading expertise cannot be disentangled in the present study. Although the present cross-sectional study could highlight associations between brain changes and reading performance, it does not allow us to infer any causal relationship. Additional studies where the developmental factors are controlled or kept constant (i.e., longitudinal designs, studies on children with the same age but different reading performances) are highly needed in order to clearly identify the consequences of reading acquisition.

5. Conclusions

The present study provides evidence that learning to read is associated with changes in the way children treat visual configurations. The better the reading performance the stronger is the involvement of the left language network in response to both written words and visual representations of objects. This seems to suggest that during reading training linguistic information can be better accessed through visual material.

Acknowledgements

This work was supported by the European Research Council [ERC-2011-ADG_20110406]; the European Union [613465-AThEME]; the Spanish Ministry of Economy and Competitiveness [PSI2015-65694-P; PSI2015-65338-P; PSI2014-54500-P]; the Spanish Government [SEV-2015-490]; and the Basque Government [PI_2015_1_25]. The AThEME project [FP7-SSH-2013-1-GA613465] has received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement no. 613465.

References

Ardilla, A., Rosselli, M., Rosas, P., 1989. Neuropsychological assessment on illiterates: visuospatial and memory abilities. Brain Cogn. 11, 147–166.

- Aylward, E.H., Park, J.E., Field, K.M., Parsons, A.C., Richards, T.L., Cramer, S.C., Meltzoff, A.N., 2005. Brain activation during face perception: evidence of a developmental change. J. Cogn. Neurosci. 17, 308–319, http://dx.doi.org/10. 1162/0898929053124884.
- Bell, A.J., Sejnowski, T.J., 1995. An information-maximization approach to blind separation and blind deconvolution. Neural Comput. 7, 1129–1159.
- Ben-Shachar, M., Dougherty, R.F., Deutsch, G.K., Wandell, B.A., 2011. The development of cortical sensitivity to visual word forms. J. Cogn. Neurosci. 23, 2387–2399, http://dx.doi.org/10.1162/jocn.2011.21615.
- Bentin, S., Mouchetant-Rostaing, Y., Giard, M.H., Echallier, J.F., Pernier, J., 1999. ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. J. Cogn. Neurosci. 11, 235–260, http://dx.doi.org/10.1162/089892999563373.
- Blau, V., Reithler, J., Van Atteveldt, N., Seitz, J., Gerretsen, P., Goebel, R., Blomert, L., 2010. Deviant processing of letters and speech sounds as proximate cause of reading failure: a functional magnetic resonance imaging study of dyslexic children. Brain 133, 868–879, http://dx.doi.org/10.1093/brain/awp308.
- Blesser, B., 1972. Speech perception under conditions of spectral transformation. I. Phonetic characteristics. J. Speech Lang. Hear. Res. 15, 5–41, http://dx.doi.org/ 10.1044/jshr.1501.05.
- Blomert, L., 2011. The neural signature of orthographic-phonological binding in successful and failing reading development. Neuroimage 57, 695–703, http:// dx.doi.org/10.1016/j.neuroimage.2010.11.003.
- Bolger, D.J., Perfetti, C.A., Schneider, W., 2005. Cross-cultural effect on the brain revisited: universal structures plus writing system variation. Hum. Brain Mapp. 25, 92–104, http://dx.doi.org/10.1002/hbm.20124.
- Brem, S., Bach, S., Kucian, K., Guttorm, T.K., Martin, E., Lyytinen, H., Brandeis, D., Richardson, U., 2010. Brain sensitivity to print emerges when children learn letter-speech sound correspondences. Proc. Natl. Acad. Sci. U. S. A. 107, 7939–7944, http://dx.doi.org/10.1073/pnas.0904402107.
- Carreiras, M., Seghier, M.L., Baquero, S., Estévez, A., Lozano, A., Devlin, J.T., Price, C.J., 2009. An anatomical signature for literacy. Nature 461, 983–986, http://dx. doi.org/10.1038/nature08461.
- Carreiras, M., Armstrong, B., Perea, M., Frost, R., 2014. The what, when, where, and how of visual word recognition. Trends Cogn. Sci. 18, 90–98, http://dx.doi.org/ 10.1016/j.tics.2013.11.005.
- Carreiras, M., Monahan, P.J., Lizarazu, M., Duñabeitia, J.A., Molinaro, N., 2015. Numbers are not like words: different pathways for literacy and numeracy. Neuroimage 18, 79–89, http://dx.doi.org/10.1016/j.neuroimage.2015.06.021.
- Castles, A., Coltheart, M., 2004. Is there a causal link from phonological awareness to success in learning to read? Cognition 91, 77–111, http://dx.doi.org/10. 1016/S0010-0277(03)00164-1.
- Castro-Caldas, A., Petterson, K.M., Reis, A., Stone-Elander, S., Ingvar, M., 1998. The illiterate brain: learning to read and write during childhood influences the functional organization of the adult brain. Brain 121, 1053–1063, http://dx.doi. org/10.1093/brain/121.6.1053.
- Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., Michel, F., 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123, 291–307, http://dx.doi.org/10.1093/brain/123. 2.291.
- Cornelissen, P.L., Kringelbach, M.L., Ellis, A.W., Whitney, C., Holliday, I.E., Hansen, P.C., 2009. Activation of the left inferior frontal gyrus in the first 200 ms of reading: evidence from magnetoencephalography (MEG). PLoS One 4 (4), e5359, http://dx.doi.org/10.1371/journal.pone.0005359.
- Dawson, G., Carver, L., Meltzoff, A.N., Panagiotides, H., McPartland, J., Webb, S.J., 2002. Neural correlates of face and object recognition in young children with autism spectrum disorder, developmental delay, and typical development. Child Dev. 73, 700–717, http://dx.doi.org/10.1111/1467-8624.00433.
- Dehaene, S., Pegado, F., Braga, L.W., Ventura, P., Nunes Filho, G., Jobert, A., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., Cohen, L., 2010. How learning to read changes the cortical networks for vision and language. Science 3, 1359–1364, http://dx.doi.org/10.1126/science.1194140.
- Dehaene, S., Cohen, L., Morais, J., Kolinsky, R., 2015. Illiterate to literate: behavioural and cerebral changes induced by reading acquisition. Nat. Rev. Neurosci. 16, 234–244, http://dx.doi.org/10.1038/nrn3924.
- Dehaene, S., 2011. The massive impact of literacy on the brain and its
- consequences for education. Hum. Neuroplasticty Edication 117, 19–32. Diedenhofen, B., Musch, J., 2015. Cocor: a comprehensive solution for the statistical comparison of correlations. PLoS One 10 (4), e0121945, http://dx. doi.org/10.1371/journal.pone.0121945.
- Dundas, E.M., Plaut, D.C., Behrmann, M., 2013. The joint development of hemispheric lateralization for words and faces. J. Exp. Psychol. Gen. 142, 348–358, http://dx.doi.org/10.1037/a0029503.
- Franklin, A., Drivonikou, G.V., Bevis, L., Davies, I.R.L., Kay, P., Regier, T., 2008. Categorical perception of color is lateralized to the right hemisphere in infants, but to the left hemisphere in adults. Proc. Natl. Acad. Sci. U. S. A. 105, 3221–3225, http://dx.doi.org/10.1073/pnas.0712286105.
- Friedman, D., Sutton, S., Putnam, L., Brown, C.J., Erlenmeyer-Kimling, L., 1988. ERP components in picture matching in children and adults. Psychophysiology 25, 570–590, http://dx.doi.org/10.1111/j.1469 -8986.1988.tb01893.x.
- Friedman, D., Putnam, L., Ritter, W., Hamberger, M., Berman, S., 1992. A developmental event-related potential study of picture matching in children, adolescents, and young adults: a replication and an extension. Psychophysiology 29, 593–610, http://dx.doi.org/10.1111/j.1469-8986.1992. tb02035.x.

- Gathers, A.D., Bhatt, R., Corbly, C.R., Farley, A.B., Joseph, J.E., 2004. Developmental shifts in cortical loci for face and object recognition. Neuroreport 15, 1549–1553, http://dx.doi.org/10.1097/01.wnr.000013329984901.86.
- Glezer, L.S., Kim, J., Rule, J., Jiang, X., Riesenhuber, M., 2015. Adding words to the brain's visual dictionary: novel word learning selectively sharpens orthographic representations in the VWFA. J. Neurosci. 35, 4965–4972, http:// dx.doi.org/10.1523/JNEUROSCI.4031-14.2015.
- Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reis, A., Eberhardt, J.L., Gabrieli, J.D., Grill-Spector, K., 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. Nat. Neurosci. 10, 512–522, http://dx.doi.org/10.1038/nn1865.
- Goswami, U., Gerson, D., Astruc, L., 2009. Amplitude envelope perception, phonology and prosodic sensitivity in children with developmental dyslexia. Read. Writing 23, 995–1019. http://dx.doi.org/10.1007/s11145-009-9186-6.
- Read. Writing 23, 995–1019, http://dx.doi.org/10.1007/s11145-009-9186-6.
 Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., Malach, R., 1998. A sequence of object-processing stages revealed by fMRI in the human occipital lobe. Hum. Brain Mapp. 6, 316–328, http://dx.doi.org/10.1002/(SICI)1097-0193.
- Hashimoto, R., Sakai, K.L., 2004. Learning letters in adulthood: direct visualization of cortical plasticity for forming a new link between orthography and phonology. Neuron 42, 311–322, http://dx.doi.org/10.1016/S0896-6273(04)00196-5.
- He, W., Brock, J., Johnson, B.W., 2015. Face processing in the brains of pre-school aged children measured with MEG. Neuroimage 106, 317–327, http://dx.doi. org/10.1016/j.neuroimage.2014.11.029.
- Helenius, P., Tarkiainen, A., Cornelissen, P., Hansen, P.C., Salmelin, R., 1999. Dissociation of normal feature analysis and deficient processing of letter-strings in dyslexic adults. Cereb. Cortex 9, 476–483, http://dx.doi.org/10. 1093/cercor/9.5.476.
- Helenius, P., Parviainen, T., Paetau, R., Salmelin, R., 2009. Neural processing of spoken words in specific language impairment and dyslexia. Brain 132, 1918–1927, http://dx.doi.org/10.1093/brain/awp134.
- Hornickel, J., Skoe, E., Nicol, T., Zecker, S., Kraus, N., 2009. Subcortical differentiation of stop consonants relates to reading and speech-in-noise perception. Proc. Natl. Acad. Sci. 106, 13022–13027, http://dx.doi.org/10.1073/ pnas.0901123106.
- Houdé, O., Rossi, S., Lubin, A., Joliot, M., 2010. Mapping numerical processing, reading, and executive functions in the developing brain: an fMRI meta-analysis of 52 studies including 842 children. Dev. Sci. 13, 876–885, http://dx.doi.org/10.1111/j.1467-7687.2009.00938.x.
- Hoving, K.L., Morin, R.E., Konick, D.S., 1974. Age-related changes in the effectiveness of name and visual codes in recognition memory. J. Exp. Child Psychol. 18, 349–361, http://dx.doi.org/10.1016/0022-0965(74)90114-3.
- Huettig, F., Mishra, R., 2014. How literacy acquisition affects the illiterate mind. A critical examination of theories and evidence. Lang. Ling. Compass 8/10, 401–427, http://dx.doi.org/10.1111/lnc3.12092.
- Jobard, G., Crivello, F., Tzourio-Mazoyer, N., 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. Neuroimage 20, 693-712, http://dx.doi.org/10.1016/S1053-8119(03)00343-4.
- Kolinsky, R., Morais, J., Content, A., Cary, L., 1987. Finding parts within figures: a developmental study. Perception 16, 399–407, http://dx.doi.org/10.1068/ p160399.
- Kolinsky, R., Morais, J., Brito-Mendes, C., 1990. Embeddedness effects on part verification in children and unschooled adults. Psychol. Belgica 30, 49–64.
- Kolinsky, R., Verhaeghe, A., Fernandes, T., Mengarda, E.J., Grimm-Cabral, L., Morais, J., 2011. Enantiomorphy through the looking glass: literacy effects on mirror-image discrimination. J. Exp. Psychol. 140, 210–238, http://dx.doi.org/ 10.1037/a0022168.
- Kremin, H., Deloche, G., Metz-Lutz, M.N., Hannequin, D., Dordain, M., Perrier, D., Cardebat, D., Ferrand, I., Larroque, C., Naud, E., Pichard, B., Bunel, G., 1991. The effect of age, educational background and sex on confrontation naming in normals: principles for testing naming ability. Aphasiology 5, 579–582, http:// dx.doi.org/10.1080/02687039108248566.
- Lizarazu, M., Lallier, M., Molinaro, N., Bourguignon, M., Paz-Alonso, P., Lerma-Usabiaga, G., Carreiras, M., 2015. Developmental evaluation of atypical auditory sampling in dyslexia: functional and structural evidence. Hum. Brain Mapp. 36, 4986–5002, http://dx.doi.org/10.1002/hbm.22986.
- Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B.H., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. U. S. A. 92, 8135–8139, http://dx.doi.org/10.1073/pnas.92. 18.8135.
- Manly, J.J., Jacobs, D.M., Sano, M., Bell, K., Merchant, C.A., Small, S.A., Stern, Y., 1999. Effect of literacy on neuropsychological test performance in nondemented, education-matched elders. J. Int. Neuropsychol. Soc. 5 (3), 191–202.
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190, http://dx.doi.org/10.1016/j. jneumeth.2007.03.024.
- Martin, A., Schurz, M., Kronbichler, M., Richlan, F., 2015. Reading in the brain of children and adults: a meta-analysis of 40 functional magnetic resonance imaging studies. Hum. Brain Mapp. 36, 1963–1981, http://dx.doi.org/10.1002/ hbm.22749.
- Maurer, U., Brem, S., Bucher, K., Brandeis, D., 2005. Emerging neurophysiological specialization for letter strings. J. Cogn. Neurosci. 17, 1532–1552, http://dx.doi. org/10.1162/089892905774597218.

- Maurer, U., Brem, S., Kranz, F., Bucher, K., Benz, R., Halder, P., Steinhausen, H.C., Brandeis, D., 2006. Coarse neural tuning for print peaks when children learn to read. Neuroimage 33, 749–758, http://dx.doi.org/10.1016/j.neuroimage.2006. 06.025.
- McCandliss, B.D., Cohen, L., Dehaene, S., 2003. The visual word form area:expertise for reading in the fusiform gyrus. Trends Cogn. Sci. 7, 293–299, http://dx.doi. org/10.1016/S1364-6613(03)00134-7.
- Molinaro, N., Lizarazu, M., Lallier, M., Bourguignon, M., Carreiras, M., 2016. Out-of-synchrony speech entrainment in developmental dyslexia. Hum. Brain Mapp. 37, 2767–2783, http://dx.doi.org/10.1002/hbm.23206.
- Monzalvo, K., Dehaene-Lambertz, G., 2013. How reading acquisition changes children's spoken language network. Brain Lang. 127, 356–365, http://dx.doi. org/10.1016/j.bandl.2013.10.009.
- Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., Dehaene-Lambertz, G., 2012. Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. Neuroimage 15, 258–274, http://dx.doi.org/10.1016/j. neuroimage.2012.02.035.
- Morais, J., Cary, L., Alegria, J., Bertelson, P., 1979. Does awareness of speech as a sequence of phones arise spontaneously? Cognition 7, 323–331, http://dx.doi. org/10.1016/0010-0277(79)90020-9.
- Morais, J., Bertelson, P., Cary, L., Alegria, J., 1986. Literacy training and speech segmentation. Cognition 24, 45–64, http://dx.doi.org/10.1016/0010-0277(86)90004-1.
- Morais, J., Castro, S.L., Scliar-Cabral, L., Kolinsky, R., Content, A., 2007. The effects of literacy on the recognition of dichotic words. Hum. Exp. Psychol., 451–465, http://dx.doi.org/10.1080/14640748708401798.
- Nishimura, M., Scherf, S., Behrmann, M., 2009. Development of object recognition in humans. Biol. Rep. 1–56, http://dx.doi.org/10.3410/b1-56.
- Obleser, J., Wise, R.J.S., Dresner, M.A., Scott, S.K., 2007. Functional integration across brain regions improves speech perception under adverse listening conditions. J. Neurosci. 27, 2283–2289, http://dx.doi.org/10.1523/JNEUROSCI. 4663-06.2007.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: open source software for advantage analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. 2011, 156869–156878, http://dx.doi.org/10. 1155/2011/156869.
- Pattamadilok, C., Knierim, I.N., Duncan, K.J.K., Devlin, J.T., 2010. How does learning to read affect speech perception? J. Neurosci. 23, 8435–8444, http://dx.doi.org/ 10.1523/JNEUROSCI.5791-09.2010.
- Pearson, K., Filon, L.N.G., 1898. Mathematical contributions to the theory of evolution IV On the probable errors of frequency constants and on the influence of random selection on variation and correlation. Philos. Trans. R. Soc. Lond. A 191, 229–311.
- Pegado, F., Comerlato, E., Ventura, F., Jobert, A., Nakamura, K., Buiatti, M., Ventura, P., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., Braga, L.W., Cohen, L., Dehaene, S., 2014. Timing the impact of literacy on visual processing. Proc. Natl. Acad. Sci. U. S. A. 111, E5233–E5242, http://dx.doi.org/10.1073/pnas. 1417347111.
- Perre, L., Bertrand, D., Ziegler, J.C., 2011. Literacy affects spoken language in a non-Linguistic task: an ERP study. Front. Psychol. 2, 1–8, http://dx.doi.org/10. 3389/fpsyg.2011.00274.
- Pinel, P., Lalanne, C., Bourgeron, T., Fauchereau, F., Poupon, C., Artiges, E., Le Bihan, D., Dehaene-Lambertz, G., Dehaene, S., 2015. Genetic and environmental influences on the visual word form and fusiform face areas. Cereb. Cortex 25, 2478–2493, http://dx.doi.org/10.1093/cercor/bhu048.
- Price, C.J., Devlin, J.T., 2011. The interactive account of ventral occipitotemporal contributions to reading. Trends Cogn. Sci. 15, 246–253, http://dx.doi.org/10. 1016/j.tics.2011.04.001.
- Pugh, K.R., Landi, N., Preston, J.L., Mencl, W.E., Austin, A.C., Sibley, D., Fulbright, R.K., Seidenberg, M.S., Grigorenko, E.L., Constable, R.T., Molfese, P., Frost, S.J., 2013. The relationship between phonological and auditory processing and brain organization in beginning readers. Brain Lang. 125, 173–183, http://dx.doi.org/ 10.1016/j.bandl.2012.04.004.
- Reis, A., Guerriero, M., Castro-Caldas, A., 1994. Influence of educational level of non brain-damaged subjects on visual naming capacities. J. Clin. Exp. Neuropsychol. 16, 939–942, http://dx.doi.org/10.1080/01688639408402705.
- Reis, A., Petersson, K.M., Castro-Caldas, A., Ingvar, M., 2001. Formal schooling influences two- but not three-dimensional naming skills. Brain Cogn. 47, 397–411, http://dx.doi.org/10.1006/brcg.2001.1316.
- Reis, A., Faísca, L., Ingvar, M., Petersson, K.M., 2006. Color makes a difference: two-dimensional object naming in literate and illiterate subjects. Brain Cogn. 60, 49–54, http://dx.doi.org/10.1016/j.bandc.2005.09.012.
- Sadat, J., Martin, C.D., Costa, A., Alario, F.X., 2014. Reconciling phonological neighborhood effects in speech production through single trial analysis. Cognit. Psychol. 68, 33–58, http://dx.doi.org/10.1016/j.cogpsych.2013.10.001.
- Salmelin, R., Helenius, P., Service, E., 2000. Neurophysiology of fluent and impaired reading: a magnetoencephalographic approach. J. Clin. Neurophysiol. 17, 163–174, http://dx.doi.org/10.1097/00004691-200003000-00005.
- Scherf, K.S., Behrmann, M., Humphreys, K., Luna, B., 2007. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. Dev. Sci. 10, F15–F30, http://dx.doi.org/10.1111/j. 1467-7687.2007.00595.x.
- Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing: a positron emission tomography study. Brain 115, 15–36, http://dx.doi.org/10.1093/brain/115.1.15.

- Shaywitz, B.A., Shaywitz, S.E., Pugh, K.R., Mencl, W.E., Fulbright, R.K., Skudlarski, P., Constable, R.T., Marchione, K.E., Fletcher, J.M., Lyon, G.R., Gore, J.C., 2002. Disruption of posterior brain systems for reading in children with developmental dyslexia. Biol. Psychiatry 52, 101–110, http://dx.doi.org/10. 1016/S0006-3223(02)01365-3.
- Simos, P.G., Breier, J.I., Zouridakis, G., Papanicolaou, A.C., 1998. Identification of language-Specific brain activity using magnetoencephalography. J. Clin. Exp. Neuropsychol. 20, 706–722, http://dx.doi.org/10.1076/jcen.20.5.706.1127.
- Simos, P.G., Papanicolaou, A.C., Breier, J.I., Wheless, J.W., Constantinou, J.E., Gormley, W.B., Maggio, W.W., 1999. Localization of language-specific cortex by using magnetic source imaging and electrical stimulation mapping. J. Neurosurg. 91, 787–796.
- Simos, P.G., Breier, J.I., Fletcher, J.M., Bergman, E., Papanicolaou, A.C., 2000. Cerebral mechanisms involved in word reading in dyslexic children: a magnetic source imaging approach. Cereb. Cortex 10, 809–816, http://dx.doi.org/10.1093/ cercor/10.8.809.
- Song, Y., Hu, S., Li, X., Li, W., Liu, J., 2010. The role of top-down task context in learning to perceive objects. J. Neurosci. 30, 9869–9876, http://dx.doi.org/10. 1523/JNEUROSCI.0140-10.2010.
- Szwed, M., Ventura, P., Querido, L., Cohen, L., Dehaene, S., 2012. Reading acquisition enhances an early visual process of contour integration. Dev. Sci. 15, 139–149, http://dx.doi.org/10.1111/j.1467-7687.2011.01102.x.
- Taulu, S., Hari, R., 2009. Removal of magnetoencephalographic artifacts with temporal signal-space separation: demonstration with single-trial auditory-evoked responses. Hum. Brain Mapp. 30, 1524–1534, http://dx.doi. org/10.1002/hbm.20627.
- Taulu, S., Kajola, M., 2005. Presentation of electromagnetic multichannel data: the signal space separation method. J. Appl. Phys. 97, 124905–124910, http://dx. doi.org/10.1063/1.1935742.

- Turkeltaub, P.E., Gareau, L., Flowers, D.L., Zeffiro, T.A., Eden, G.F., 2003. Development of neural mechanisms for reading. Nat. Neurosci. 6, 767–773, http://dx.doi.org/10.1038/nn1065.
- Ventura, P., Fernandes, T., Cohen, L., Morais, J., Kolinsky, R., Dehaene, S., 2013. Literacy acquisition reduces the influence of automatic holistic processing of faces and houses. Neurosci. Lett. 554, 105–109, http://dx.doi.org/10.1016/j. neulet.2013.08.068.
- Vilberg, K.L., Davachi, L., 2013. Perirhinal-hippocampal connectivity during reactivation is a marker for object-based memory consolidation. Neuron 79, 1232–1242, http://dx.doi.org/10.1016/j.neuron.2013.07.013.
- Woodhead, Z.V.J., Barnes, G.R., Penny, W., Moran, R., Teki, S., Price, C.J., Leff, A.P., 2014. Reading front to back: MEG evidence for early feedback effects during word recognition. Cereb. Cortex 24, 817–825, http://dx.doi.org/10.1093/ cercor/bbs365.
- Woodruff, C.K., White-Schwoch, T., Tierney, A.T., Strait, D.L., Kraus, N., 2014. Beat synchronization predicts neural speech encoding and reading readiness in preschoolers. Proc. Natl. Acad. Sci. 111, 14559–14564, http://dx.doi.org/10. 1073/pnas.1406219111.
- Xue, G., Chen, C., Jin, Z., Dong, Q., 2006. Language experience shapes fusiform activation when processing a logographic artificial language: an fMRI training study. Neuroimage 31, 1315–1326, http://dx.doi.org/10.1016/j.neuroimage. 2005.11.055.
- Yoncheva, Y.N., Blau, V.C., Maurer, U., McCandliss, B.D., 2010. Attentional focus during learning impacts N170 ERP responses to an artificial script. Dev. Neuropsychol. 35, 423–445, http://dx.doi.org/10.1080/87565641.2010.480918.