

Neural Responses of the Anterior Ventral Occipitotemporal Cortex in Developmental Dyslexia: Beyond the Visual Word Form Area

Ana Pina Rodrigues,^{1,2} José Rebola,¹ Marcelino Pereira,³ Marieke van Asselen,¹ and Miguel Castelo-Branco^{1,2}

¹Institute for Biomedical Imaging and Life Sciences (CNC.IBIL), Faculty of Medicine, University of Coimbra, Coimbra, Portugal

²Coimbra Institute for Biomedical Imaging and Translational Research (CIBIT), Institute of Nuclear Sciences Applied to Health (ICNAS), University of Coimbra, Coimbra, Portugal

³Faculty of Psychology and Education Sciences, University of Coimbra, Coimbra, Portugal

Correspondence: Miguel Castelo-Branco, Institute for Biomedical Imaging and Life Sciences (CNC.IBIL), Faculty of Medicine, University of Coimbra, Azinhaga de Santa Comba, Coimbra 3000-548, Portugal; mcbranco@fmed.uc.pt.

APR and JR contributed equally to the work presented here and should therefore be regarded as equivalent authors.

Submitted: December 6, 2018

Accepted: February 7, 2018

Citation: Pina Rodrigues A, Rebola J, Pereira M, van Asselen M, Castelo-Branco M. Neural responses of the anterior ventral occipitotemporal cortex in developmental dyslexia: beyond the visual word form area. *Invest Ophthalmol Vis Sci.* 2019;60:1063-1068. <https://doi.org/10.1167/iovs.18-26325>

PURPOSE. For the past 2 decades, neuroimaging studies in dyslexia have pointed toward a hypoactivation of the ventral occipitotemporal cortex (VOTC), a region that has been closely associated to reading through the extraction of a representation of words which is invariant to position, size, font or case. However, most of the studies are confined to the visual word form area (VWFA), while recent studies have demonstrated a posterior-to-anterior gradient of print specificity along the VOTC. In our study, the whole VOTC, partitioned into three main patches of cortex, is assessed in dyslexic and control adults.

METHODS. A total of 30 participants were included in this study (14 developmental dyslexics and 16 age- and education-matched controls). The design consisted of alternately viewed blocks of stimuli from a given class (words, consonant strings, phase-scrambled words, phase-scrambled consonant strings, small checkerboards, large checkerboards). The analyzed contrast was print stimuli (words and consonants) versus scrambled stimuli and checkerboards.

RESULTS. Corroborating previous findings, our results showed underactivation to print stimuli in the VWFA of dyslexics. Additionally, differences between dyslexics and controls were also found, particularly in an area of the anterior partition of the VOTC, suggesting a relevant role of this area in word processing.

CONCLUSIONS. In sum, our study goes beyond the underactivation hypothesis in the VWFA of dyslexics and indicates that a particular area on the anterior fusiform region might be particularly involved in the reading deficits in dyslexia, demonstrating the involvement of multiple areas within VOTC in reading processes.

Keywords: developmental dyslexia, fMRI, visual word form area (VWFA), ventral occipitotemporal cortex (VOTC)

Developmental dyslexia (DD) is a high prevalent neurodevelopmental disorder ($\approx 10\%$)¹ characterized by a reading impairment in spite of a normal intellectual functioning and educational opportunities.² Typically, it affects the accuracy and/or fluency of word recognition as well as spelling and decoding abilities.³ The causes of this condition and the mechanisms underlying such causes remain under debate and are a subject of intensive research. Although phonologic processing deficits are well established as core deficits in DD,^{4,5} it has been suggested that visuo-perceptual impairments may also contribute to the pathophysiology of this condition.^{6,7}

Recent neuroimaging methods, including functional magnetic resonance imaging (fMRI), electroencephalography (EEG, and event-related potentials or ERPs), and magnetoencephalography (MEG), have consistently revealed the brain regions dominantly involved in single word reading,⁸ which are likely important to the characterization and understanding of the dyslexic brain. Three major circuits contributing to different

aspects of reading have been identified.⁹ A left dorsal temporoparietal circuit around the classically termed Wernicke's area is associated with phonology-based reading processes (i.e., grapheme-phoneme conversion, phonologic assembly). Additionally, a left inferior frontal circuit around the classically termed Broca's area, including inferior frontal and precentral gyri, is thought to be involved in speech-gestural articulatory recoding of print. Finally, a left ventral occipitotemporal circuit including lateral extrastriate, fusiform, and inferior temporal regions is linked to memory-based visual-orthographic word recognition.¹⁰ The latter includes the visual word form area (VWFA), which has been widely studied after being identified and described by Cohen et al.¹¹ as an area specifically tuned to process letter strings.¹¹⁻¹⁵

In particular, this last area belongs to the visual route known as the ventral "what" pathway,¹⁶ contributing to reading through the extraction of a representation of words which is invariant to position, size, font or case. This representation has been referred to in literature as the visual word form (VWF).¹⁷



Because activation in this region increases with reading skill, Shaywitz et al.¹⁸ referred to the left ventral occipitotemporal cortex (VOTC) as a “reading skill zone.” Since reading skills are impaired in dyslexia, it would be expected to find an underactivation of this region in this condition.^{3,19} In fact, in the last 2 decades, neuroimaging studies comparing fMRI activations of dyslexic and typical readers have identified an hypoactivation to print in the left VOTC compared to control subjects,^{18,20–26} particularly in the VWFA.^{27–29}

Although some authors have suggested that the dysfunctional activation of the VOTC is secondary to a primary dysfunction of the temporoparietal reading system,^{28,30,31} the relevance of this region is highlighted in a study by Richlan et al.,³² which reports the VOTC as the only area underactivated in dyslexics compared with nondyslexics in meta-analyses conducted in children as well as in adults.

Despite recent reports confirming that visual tuning follows a posterior-to-anterior gradient of increasing print specificity in the left occipitotemporal network in adults and adolescents^{33–35} as well as in children,³⁴ most VOTC studies restrict themselves to the analysis of the VWFA, even when coordinates deviate from the ones defined by the early work by Cohen et al.,^{36–39} who advert that this area is accurately found near Talairach coordinates $-43, -54, -12$, with a standard deviation of only ~ 0.5 cm in the healthy brain. In fact, this diversity was a concern already expressed by these authors, by highlighting an overview of 20 imaging studies reporting activations that fell within the following boundary coordinates: $-50 < x < -30$; $-80 < y < -30$; $z < 0$. The authors made a distinction between more anterior peaks, typically elicited by nonvisual verbal stimuli (or common to the visual and nonvisual stimuli), and the more posterior ones, consistent with their VWFA, observed when contrasting alphabetic strings with nonalphabetic stimuli such as false fonts or fixation. Posterior to this site, another word-tuned region has been identified by Strother et al.⁴⁰ who coined the name occipital word form area (see also Szwed et al.⁴¹), and advocated a role analogous to that of the occipital face area (OFA),⁴² which is devoted to processing of lower-level components or parts of the face, which are bound further upstream in the face-processing network.

According to this framework, in the present study we evaluate print tuning in dyslexic adults along multiple regions within the VOTC.

MATERIALS AND METHODS

Participants

We recruited 14 developmental dyslexics (mean age: 30.50 ± 8.73 , mean educational level: 15.64 ± 1.86) and 16 age-matched controls (mean age: 29.44 ± 6.72 , mean educational level: 16.38 ± 2.03). The inclusion criterion for the dyslexics group was a previous clinical diagnosis of developmental dyslexia and no prior history of other developmental disorders. In the control group we included adults with no history of learning, developmental, cognitive, neurologic, or neuropsychiatric disorders.

All participants were assessed in terms of reading performance and intelligence level. For the reading assessment, a subtest from the Psycholinguist Assessments of Language Processing in Aphasia - Portuguese version (PALPA-P)⁴³ was used. In this subtest, participants were asked to read a list of 60 words and pseudowords as quickly as possible. The measures obtained from this subtest were reading speed (in seconds) and accuracy (number of words correctly read). Intelligence level was measured through the Raven Progressive Matrices Test - Set 1 (RPM).⁴⁴

The groups were matched for age, sex, years of education, and IQ (as assessed by RPM), and statistically different in the reading measures (speed and accuracy). All participants were right-handed and had normal or corrected to normal vision. Participants' demographics and reading and intelligence scores are summarized in Table 1. The study was conducted in accordance with the tenets of the Declaration of Helsinki and was approved by the Ethics Committee of the Faculty of Medicine of the University of Coimbra. Written informed consent was obtained from the participants, after an explanation of the nature and possible consequences of the study.

Task and Stimuli

During fMRI acquisition, participants were asked to pay attention to presented words, consonants strings, checkerboards, and phase-scrambled versions of the words and consonant strings. Implicit processing by passive viewing was chosen to avoid confounds driven by potential differences in task performance. Though the participants are not instructed to read the word during this task, reading occurs implicitly and without conscious effort in skilled readers.⁴⁵ Various studies involving children and adults have demonstrated implicit processing activation in reading-related brain regions, including those thought to be involved in orthographic, phonologic, and semantic processing.^{45–48}

Word stimuli consisted of 60 five-letter words selected from the Portuguese Corlex database. Words with frequency values above 100 are considered to be highly frequent with the mean word frequency values for our sample being 1758.30.

Consonant strings were built by combining 60 random series of five consonants (example: ‘vcbtx’). All of the consonant strings were unpronounceable in Portuguese.

Phase-scrambled versions were built for every word and consonant stimuli, in a total of 120.

Finally, two versions of checkerboards were built. A small version spanned the exact size of the word and consonant stimuli. A larger version had a threefold increase in the horizontal dimension and a 4-fold increase in the vertical dimension. This span was originally designed for use in a separate noise interference study on dyslexic subjects (data not shown) but was nonetheless used in this study to equate the number of acquired volumes per condition. The horizontal spatial frequency of the checkerboard stimuli was equated to the word and consonant stimuli (one black and white square for each letter).

fMRI Scanning

Images were obtained on a scanner (Tim Trio 3T; Siemens Medical Solutions USA, Inc., Malvern, PA, USA) using a 12-channel head coil. Structural images were collected using a T1 weighted magnetization prepared rapid-acquisition gradient echo (TR = 2530 ms, TE = 3.42 ms, flip angle = 7, matrix size = 256×256 , voxel size = 1 mm^3 isotropic). Standard T2 n-weighted gradient-echo echo planar imaging was used for the functional task runs (TR = 1500 ms; TE = 30 ms; 3.6×3.6 mm in-plane resolution; 3.6-mm slice thickness with no gap; flip angle = 76; matrix size = 64×64 ; number of slices = 28; 285 measurements were used for the functional run). The slices were oriented to obtain a brain coverage spanning from the cerebellum to the motor cortices, ensuring ventral occipitotemporal coverage. Image processing was performed using commercial software (BrainVoyager QX v2.6; Brain Innovation, Maastricht, The Netherlands). Preprocessing steps included motion correction, slice scan-time correction, linear trend removal and temporal high-pass filtering of 0.00980 Hz (3 cycles in time course). Functional data were registered to each

TABLE 1. Summary Statistics for the Two Groups of Participants

| Demographics and Clinical Variables | Dyslexics (<i>n</i> = 14) | | | Controls (<i>n</i> = 16) | | | <i>P</i> Value |
|-------------------------------------|----------------------------|--------|-------|---------------------------|-------|------|----------------|
| | Mean | Range | SD | Mean | Range | SD | |
| Age, y | 30.50 | 20–45 | 8.73 | 29.44 | 21–48 | 6.72 | 0.710 |
| Education, y | 15.64 | 12–17 | 1.86 | 16.38 | 9–17 | 2.03 | 0.315 |
| RPM | 10.29 | 9–12 | 0.99 | 10.93 | 10–12 | 0.73 | 0.062 |
| PALPA-P reading speed, s | 75.85 | 46–101 | 16.58 | 39.31 | 29–47 | 6.43 | <0.001 |
| PALPA-P accuracy | 50.00 | 42–57 | 4.72 | 56.46 | 54–58 | 1.27 | <0.001 |
| Sex, M/F | 6/8 | | | 12/4 | | | 0.078 |

Probability values for group comparisons using *t*-tests (except for sex, for which the Chi square test was used) are reported ($P < 0.05$ values are considered significant).

individual's anatomical scan and transformed to a common Talairach space.

The functional scan consisted of alternately viewed blocks of stimuli from a given class (words, consonant strings, phase-scrambled words, phase-scrambled consonant strings, small checkerboards, large checkerboards). The run had 18 blocks (three for each category) and each block lasted 20 seconds (20 images, 800 ms each, 200 ms gap), separated by 10-second fixation baseline intervals. The run started with a period of fixation for 10 seconds and ended with a period of fixation for 30 seconds. Block presentation order was pseudorandomized within each repetition (there had to be a block of each stimulus category before a second block of a given category could be presented) and then the same order was used for all participants.

DATA ANALYSIS

GLMs and Contrasts

A general linear model (GLM) with six predictors, one for each stimulus category was built for each participant. We focused on a contrast similar to the one used by Cohen to identify the

VWFA, although we also included scrambled versions of words and consonant strings. In this manner, contrast was PRINT STIMULI (WORDS and CONSONANTS) versus SCRAMBLED STIMULI and CHECKERBOARDS.

VOTC Partitions

Following the reasoning outlined in the introduction, we parceled the VOTC into three ROIs, which approximately encompass the VWF system (among other dedicated areas): an anterior portion centered on $x = -35$; $y = -40$; $z = -20$, a middle portion centered on $x = -43$; $y = -60$; $z = -15$, and a posterior portion centered on $x = -40$; $y = -85$; $z = -5$. The regions span 25 mm along the x dimension; 20 mm along the y dimension and 30 mm along the z dimension. The posterior region was allowed a larger span along the y dimension to include posterior occipital activations.

The employment of a 3-fold division of this region in word processing studies is not new and has been successfully used by other authors.^{49,50} Furthermore, individual data corroborates this approach, as exemplified in Figure 1 for both dyslexic and control subjects. An illustration of the ROIs center and span is shown in Figure 2.

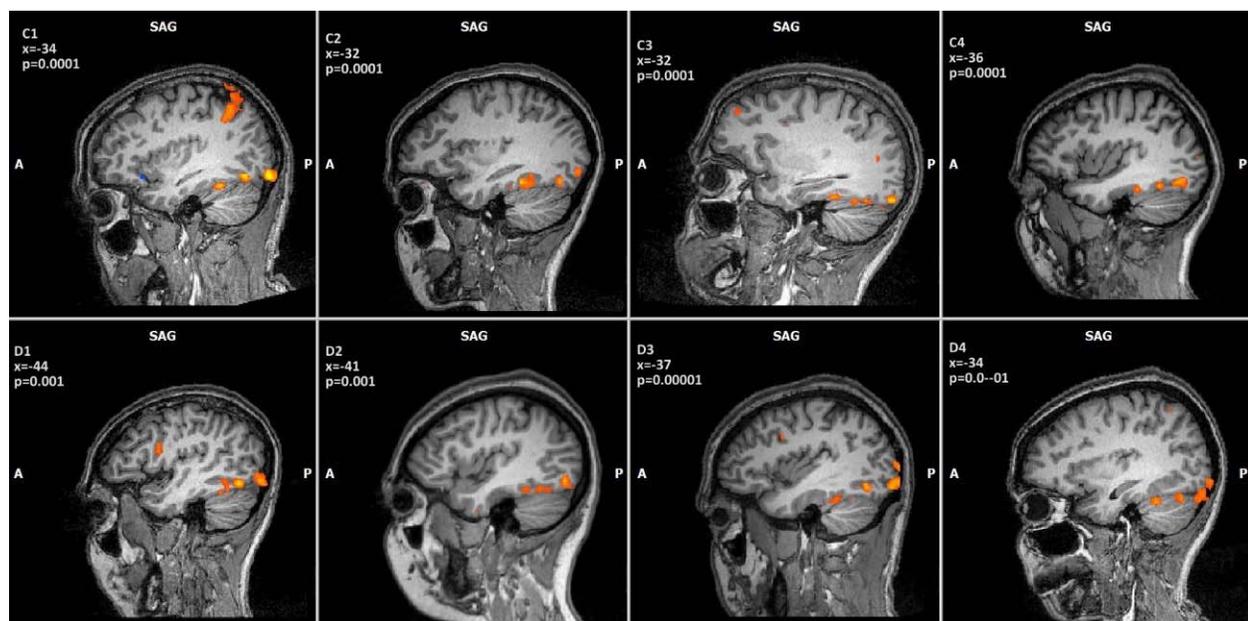


FIGURE 1. Example of individual activations to the contrast words and consonants versus scrambled stimuli and checkerboards. Four controls (*top row*) and four dyslexics (*bottom row*) are shown. Note the pattern of the three identifiable clusters.

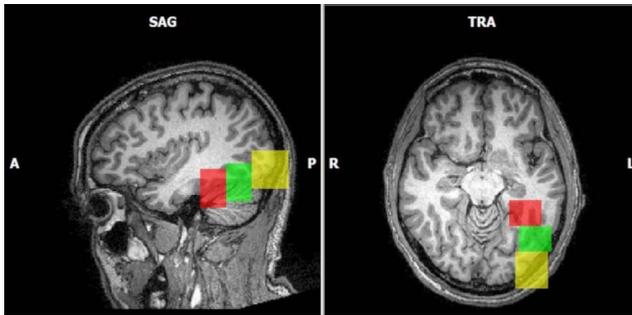


FIGURE 2. Illustration of the three selected ROIs, corresponding to three broad regions of the VOTC: posterior VOTC (yellow); middle VOTC (green); and anterior VOTC (red).

Statistical Analyses

A standard random effects analysis (RFX-GLM) to check for areas with significant differences between groups was performed. Results are evaluated for each of the three VOTC partitions, at a significance threshold of $P < 0.05$ and a cluster threshold of $8 \text{ mm}^3 (2 \times 2 \times 2)$.

RESULTS

For every VOTC partition, areas could be identified with greater activation for controls than dyslexics which are in concordance with coordinates previously reported in literature for word-processing relevant areas (see Table 2).

The significance map for the anterior partition is clearly dominated by an area in the left anterior fusiform gyrus, centered on Talairach coordinates $-31, -35, \text{ and } -18$. In the middle partition, an area with greater activity for controls than dyslexics was identified in close accordance to the reported coordinates of the VWFA ($-43, -53, -6$). For the posterior partition, dyslexics showed significant hypoactivation for print stimuli in an area in the left posterior fusiform gyrus, centered on Talairach coordinates $-34, -83, \text{ and } -12$.

Thus, according to previous findings, we found underactivation to print stimuli in the VWFA of dyslexics. Nonetheless, the major differences between dyslexics and controls were found in the anterior partition of the VOTC, indicating that the underactivation is not restricted to the VWFA. Taken together, our results show that there seem to be areas differentially recruited by controls and dyslexics in word-reading processes.

DISCUSSION

Since the early description of the VWFA in 2002, and the claim of a word tuning gradient in the VOTC, an intense debate has been generated concerning its preservation in dyslexia. Previous work has identified hypoactivation of the VOTC in the dyslexic brain, particularly in the VWFA.

In his seminal VWFA study, Cohen and colleagues reviewed word-tuned activations that ranged from $y = -80$ to $y = -30$.¹¹ In 2007, Vinckier et al.³⁵ exploited the full range of this extension to argue in favor of a hierarchical coding of letter streams in the VOTC, from $y = -96$ to $y = -40$. They established that activation became more selective for higher-level stimuli toward the anterior fusiform region. Further research confirmed both the diversity and the posterior to anterior (ranging from low-level to high-level) direction of the word-tuned gradient.^{38,41,51-53} With this in mind, in the present study, we probed print-specificity in the whole VOTC, partitioned into three regions: anterior, middle, and posterior.

Corroborating previous studies,²⁷⁻²⁹ we demonstrated that dyslexics show hypoactivation to print stimuli in the VWFA (Talairach coordinates $-43, -53, -6$). Interestingly, we identified other areas in which print-specific activity is significantly larger for controls than dyslexics, particularly in the anterior partition of the VOTC, a region which sits at the top of the VOTC visual gradient and may bridge with nearby semantic and multimodal regions (for reviews, see Refs. 54 and 55). In fact, the most robust differences were observed in an area of the anterior fusiform region (Talairach coordinates $-31, -35, -18$), which cluster size resulting from the statistical analysis suggests that this may be a distinct and relevant reading related area that would be worth investigating in future studies.

Other studies had located the brain region showing greater selectivity for letter strings in more anterior VOTC regions, rather than in the VWFA.^{47,56} Our study indicates that, adding to the VWFA, a specific area in the anterior VOTC might be particularly involved in the reading deficits in dyslexia, thus demonstrating the involvement of multiple areas within VOTC in reading processes.

According to the hierarchical coding of letter streams in the VOTC,^{33,38,41,51-53} bilateral early visual cortices extract the early features of the letters which are then recombined into increasingly abstract letter string representations up to the VWFA. The areas identified in the present study would therefore lie toward greater integration of print units, being responsible for whole word processing (VWFA) and even multimodal/semantic representation of words (anterior temporal cortex). Applying this framework to reading error analysis, disrupted neural activity at lower levels would predict errors on similar words (e.g., misreading “farm” as “form”), whereas noise at higher levels could lead to errors on increasingly larger units such that eventually the whole word is difficult to access.³⁷ In this manner, the dyslexic pattern of activation in our sample would be more associated with difficulties at the whole-word higher perceptual levels whereas lower-level perception seems to be more preserved.

Nevertheless, the functional posterior-to-anterior hierarchy in the left VOTC has recently been challenged. In a very recent work, Lochy and colleagues⁵⁸ report an extensive functional mapping of the VOTC for selective responses to visual letter strings and words with intracerebral recordings. Besides showing letter-selective responses across all the VOTC, they found responses to real words in a region extending more anteriorly than the VWFA. Moreover, a distinct spatial

TABLE 2. Mean Contrast Differences in the Three VOTC Partitions

| VOTC Partition | Print vs. Scrambled and Checkerboards | | | | | Cluster Size |
|---------------------|---------------------------------------|----------|-----------|-------|--------|--------------|
| | Controls > Dyslexics | Controls | Dyslexics | t | p | |
| Anterior partition | ($-31, -35, -18$) | 0.845 | -0.256 | 3.728 | 0.0008 | 786 |
| Middle partition | ($-43, -53, -6$) | 1.021 | 0.141 | 2.483 | 0.0193 | 48 |
| Posterior partition | ($-34, -83, -12$) | 1.354 | -0.079 | 2.318 | 0.0280 | 7 |

organization for prelexical and lexical processing in the left fusiform gyrus was not observed.

The fine grained spatial organization of the VOTC for processing letters and words is therefore still under debate, although our study and others suggest that the contribution of multiple areas, in particular in anterior VOTC, is relevant. In addition to the VWFA, future studies are needed to unveil the specific contribution to reading of other areas along the VOTC.

Acknowledgments

Supported by the Foundation for Science and Technology Portugal under Grants [PTDC/SAU-NSC/113471/2009], [SFRH/BD/75083/2010] and UID/NEU/04539/2013-COMPETE, POCL01-0145-FED-ER-007440.

Disclosure: **A. Pina Rodrigues**, None; **J. Rebola**, None; **M. Pereira**, None; **M. van Asselen**, None; **M. Castelo-Branco**, None

References

- Rutter M, Caspi A, Fergusson D, et al. Sex differences in developmental reading disability. *JAMA*. 2004;291:2007-2012.
- American Psychiatric Association. *Diagnostic and Statistical Manual of Mental Disorders (DSM-IV-TR)*. 4th ed. Washington DC: American Psychiatric Association; 2000.
- Shaywitz SE, Shaywitz BA. Dyslexia (specific reading disability). *Biol Psychiatry*. 2005;57:1301-1309.
- Snowling MJ. From language to reading and dyslexia. *Dyslexia*. 2001;7:37-46.
- Vellutino FR, Fletcher JM, Snowling MJ, Scanlon DM. Specific reading disability (dyslexia): what have we learned in the past four decades? *J Child Psychol Psychiatry*. 2004;45:2-40.
- Stein J, Walsh V. To see but not to read; the magnocellular theory of dyslexia. *Trends Neurosci*. 1997;20:147-152.
- Stein J. The magnocellular theory of developmental dyslexia. *Dyslexia*. 2001;7:12-36.
- Norton ES, Beach SD, Gabrieli JDE. Neurobiology of dyslexia. *Curr Opin Neurobiol*. 2015;30:73-78.
- Pugh KR, Mencl WE, Jenner AR, et al. Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Ment Retard Dev Disabil Res Rev*. 2000;6:207-213.
- Martin A, Schurz M, Kronbichler M, Richlan F. Reading in the brain of children and adults: a meta-analysis of 40 functional magnetic resonance imaging studies. *Hum Brain Mapp*. 2015;36:1963-1981.
- Cohen L, Lehericy S, Chochon F, Lemer C, Rivaud S, Dehaene S. Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain*. 2002;125:1054-1069.
- Cohen L, Dehaene S, Naccache L, et al. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*. 2000;123:291-307.
- Cohen L, Dehaene S. Specialization within the ventral stream: the case for the visual word form area. *Neuroimage*. 2004;22:466-476.
- Dehaene S, Cohen L. The unique role of the visual word form area in reading. *Trends Cogn Sci*. 2011;15:254-262.
- Dehaene S, Le Clec'h G, Poline JB, Le Bihan D, Cohen L. The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport*. 2002;13:321-325.
- Ungerleider LG, Mishkin M. Two cortical visual systems. In: Ingle D, Goodale M, Mansfield R, eds. *The Analysis of Visual Behavior*. Cambridge, MA: MIT Press; 1982:549-586.
- Warrington EK, Shallice T. Word-form dyslexia. *Brain*. 1980;103:99-112.
- Shaywitz BA, Shaywitz SE, Pugh KR, et al. Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biol Psychiatry*. 2002;52:101-110.
- Sandak R, Mencl WR, Frost SJ, Pugh KR. The neurobiological basis of skilled and impaired reading: recent findings and new directions. *Sci Stud Read*. 2004;8:273-292.
- Maurer U, Brem S, Bucher K, et al. Impaired tuning of a fast occipito-temporal response for print in dyslexic children learning to read. *Brain*. 2007;130:3200-3210.
- Cao F, Bitan T, Chou T, Burman DD, Booth JR. Deficient orthographic and phonological representations in children with dyslexia revealed by brain activation patterns. *J Child Psychol Psychiatry*. 2006;47:1041-1050.
- Paulesu E, Démonet JF, Fazio F, et al. Dyslexia: cultural diversity and biological unity. *Science*. 2001;291:2165-2167.
- Brunswick N. Explicit and implicit processing of words and pseudowords by adult developmental dyslexics: a search for Wernicke's Wortschatz? *Brain*. 1999;122:1901-1917.
- Rumsey JM, Horwitz B, Donohue BC, Nace K, Maisog JM, Andreasen P. Phonological and orthographic components of word recognition. A PET-rCBF study. *Brain*. 1997;120:739-759.
- Salmelin R, Service E, Kiesilä P, Uutela K, Salonen O. Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Ann Neurol*. 1996;40:157-162.
- Kronbichler L, Kronbichler M. The importance of the left occipitotemporal cortex in developmental dyslexia. *Curr Dev Disord Reports*. 2018;5:1-8.
- Martin A, Kronbichler M, Richlan F. Dyslexic brain activation abnormalities in deep and shallow orthographies: a meta-analysis of 28 functional neuroimaging studies. *Hum Brain Mapp*. 2016;37:2676-2699.
- Boros M, Anton J-L, Pech C, Grainger J, Szwed M, Ziegler JC. Orthographic processing deficits in developmental dyslexia: beyond the ventral visual stream. *Neuroimage*. 2016;128:316-327.
- van der Mark S, Klaver P, Bucher K, et al. The left occipitotemporal system in reading: disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. *Neuroimage*. 2011;54:2426-2436.
- Pugh KR, Mencl WE, Jenner AR, et al. Neurobiological studies of reading and reading disability. *J Commun Disord*. 2001;34:479-492.
- McCandliss BD, Noble KG. The development of reading impairment: a cognitive neuroscience model. *Ment Retard Dev Disabil Res Rev*. 2003;9:196-205.
- Richlan F, Kronbichler M, Wimmer H. Meta-analyzing brain dysfunctions in dyslexic children and adults. *Neuroimage*. 2011;56:1735-1742.
- Vinckier F, Dehaene S, Jobert A, Dubus JP, Sigman M, Cohen L. Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron*. 2007;55:143-156.
- Brem S, Halder P, Bucher K, Summers P, Martin E, Brandeis D. Tuning of the visual word processing system: distinct developmental ERP and fMRI effects. *Hum Brain Mapp*. 2009;30:1833-1844.
- Brem S, Bucher K, Halder P, et al. Evidence for developmental changes in the visual word processing network beyond adolescence. *Neuroimage*. 2006;29:822-837.
- Reinke K, Fernandes M, Schwindt G, O'Craven K, Grady CL. Functional specificity of the visual word form area: general activation for words and symbols but specific network activation for words. *Brain Lang*. 2008;104:180-189.
- James KH, James TW, Jobard G, Wong ACN, Gauthier I. Letter processing in the visual system: different activation patterns

- for single letters and strings. *Cogn Affect Behav Neurosci*. 2005;5:452-466.
38. Barton JJS, Fox CJ, Sekunova A, Iaria G. Encoding in the visual word form area: an fMRI adaptation study of words versus handwriting. *J Cogn Neurosci*. 2010;22:1649-1661.
 39. Cavina-Pratesi C, Large ME, Milner AD. Reprint of: visual processing of words in a patient with visual form agnosia: a behavioural and fMRI study. *Cortex*. 2015;72:97-114.
 40. Strother L, Coros AM, Vilis T. Visual cortical representation of whole words and hemifield-split word parts. *J Cogn Neurosci*. 2016;28:252-260.
 41. Szwed M, Dehaene S, Kleinschmidt A, et al. Specialization for written words over objects in the visual cortex. *Neuroimage*. 2011;56:330-344.
 42. Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW. The fusiform "face area" is part of a network that processes faces at the individual level. *J Cogn Neurosci*. 2000;12:495-504.
 43. Castro SL, Caló S, Gomes I. *PALPA-P - Provas de Avaliação da Linguagem e da Afasia em Português*. Lisboa: CEGOC; 2007.
 44. Raven J, Court J, Raven J. *Manual for Raven's Progressive Matrices*. London: H. K. Lewis; 1976.
 45. Price CJ, Wise RJS, Frackowiak RSJ. Demonstrating the implicit processing of visually presented words and pseudo-words. *Cereb Cortex*. 1996;6:62-70.
 46. Ben-Shachar M, Dougherty RF, Deutsch GK, Wandell BA. The development of cortical sensitivity to visual word forms. *J Cogn Neurosci*. 2011;23:2387-2399.
 47. Turkeltaub PE, Gareau L, Flowers DL, Zeffiro TA, Eden GF. Development of neural mechanisms for reading. *Nat Neurosci*. 2003;6:767-773.
 48. Turkeltaub PE, Flowers DL, Verbalis A, Miranda M, Gareau L, Eden GF. The neural basis of hyperlexic reading: an fMRI case study. *Neuron*. 2004;41:11-25.
 49. Seghier ML, Price CJ. Explaining left lateralization for words in the ventral occipitotemporal cortex. *J Neurosci*. 2011;31:14745-53.
 50. Mei L, Xue G, Lu Z-L, et al. Long-term experience with Chinese language shapes the fusiform asymmetry of English reading. *Neuroimage*. 2015;110:3-10.
 51. Zemmoura I, Herbert G, Moritz-Gasser S, Duffau H. New insights into the neural network mediating reading processes provided by cortico-subcortical electrical mapping. *Hum Brain Mapp*. 2015;36:2215-230.
 52. van der Mark S, Bucher K, Maurer U, et al. Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. *Neuroimage*. 2009;47:1940-1949.
 53. Olulade OA, Flowers DL, Napoliello EM, Eden GF. Dyslexic children lack word selectivity gradients in occipito-temporal and inferior frontal cortex. *NeuroImage Clin*. 2015;7:742-754.
 54. Binder JR, Desai RH, Graves WW, Conant LL. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex*. 2009;19:2767-2796.
 55. Jobard G, Vigneau M, Mazoyer B, Tzourio-Mazoyer N. Impact of modality and linguistic complexity during reading and listening tasks. *Neuroimage*. 2007;34:784-800.
 56. Olulade OA, Flowers DL, Napoliello EM, Eden GF. Developmental differences for word processing in the ventral stream. *Brain Lang*. 2013;125:134-145.
 57. Glezer LS, Jiang X, Riesenhuber M. Evidence for highly selective neuronal tuning to whole words in the "visual word form area." *Neuron*. 2009;62:199-204.
 58. Lochy A, Jacques C, Maillard L, Colnat-Coulbois S, Rossion B, Jonas J. Selective visual representation of letters and words in the left ventral occipito-temporal cortex with intracerebral recordings. *Proc Natl Acad Sci*. 2018;115:E7595-E7604.