Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

When transparency is opaque: Effects of diacritic marks and vowel letters on dyslexic Hebrew readers

Yael Weiss [a], Tami Katzir [b] and Tali Bitan [c,*]

[a] Department of Communication Sciences and Disorders, University of Texas at Austin, Austin, TX, USA
[b] Department of Learning Disabilities, The E.J. Safra Brain Research Center for the Study of Learning Disabilities, University of Haifa, Israel
[c] Psychology Department and Institute for Information Processing and Decision Making, University of Haifa, Israel

ARTICLE INFO

Article history:
Received 3 November 2015
Reviewed 2 February 2016
Revised 16 May 2016
Accepted 19 July 2016
Action editor Roberto Cubelli
Published online 29 July 2016

Keywords:
fMRI
Dyslexia
Orthographic transparency
Familiarity
Phonology

ABSTRACT

The current study examined the effects of orthographic transparency and familiarity on brain mechanisms involved in word recognition in adult dyslexic Hebrew readers. We compared functional Magnetic Resonance Imaging (fMRI) brain activation in 21 dyslexic readers and 22 typical readers, and examined the effects of diacritic marks that provide transparent but less familiar information and vowel letters that increase orthographic transparency without compromising familiarity. Dyslexic readers demonstrated reduced activation in left supramarginal gyrus (SMG) as compared to typical readers, as well as different patterns of activation within the left inferior frontal gyrus (IFG). Furthermore, in contrast to typical readers, dyslexic readers did not show increased activation for diacritics in left temporo-parietal junction regions, associated with mapping orthography to phonology. Nevertheless, both groups showed the facilitation effect of vowel letters on regions associated with lexical-semantic access. Altogether the results suggest that while typical readers can compensate for the reduced familiarity of pointed words with increased reliance on decoding of smaller units, dyslexic readers do not, and therefore they show a higher cost.

1. Introduction

Studies across different alphabetical orthographies show deficient phonological processing in individuals with dyslexia (Paulesu et al., 2001; Stanovich, 1988; Ziegler & Goswami, 2005; Ziegler, Perry, Ma-Wyatt, Ladner, & Schulte-Körne, 2003). Phonological processes are those involved in the representation, analysis, and manipulation of information specifically related to linguistic sounds from the level of the individual speech sound, or phoneme, all the way to the level of connected text (Katzir, Christodoulou, & Chang, in press; Katzir, Misra, & Poldrack, 2005). Hence, dyslexic children often have difficulty developing an awareness that words, both written

* *Corresponding author*. Psychology Department and Institute for Information Processing and Decision Making, University of Haifa, 199 Aba Khoushy Avenue, Mount Carmel, Haifa 3498838, Israel.
E-mail addresses: yael.weiss@austin.utexas.edu (Y. Weiss), katzirta@gmail.com (T. Katzir), tbitan@research.haifa.ac.il (T. Bitan).
http://dx.doi.org/10.1016/j.cortex.2016.07.017
0010-9452/

and spoken, can be broken down into smaller units of sounds, such as phonemes, onsets, rhymes and syllables (Torgesen, Wagner, & Rashotte, 1994; Wolf & Kennedy, 2003). While different sub-types of dyslexia exist (Castles, Bates, & Coltheart, 2006; Castles & Coltheart, 1993; Hadzibeganovic et al., 2010; Manis, Seidenberg, Doi, McBride-Chang, & Petersen, 1996; Wolf & Bowers, 1999; Zoccolotti & Friedmann, 2010) the phonological deficit appears to be widely associated with dyslexia (Ziegler & Goswami, 2005).

In transparent orthographies (in which grapheme to phoneme correspondence is consistent), such as German, readers tend to rely on processing at the small grain-size level, whereas in less transparent orthographies, such as English, readers tend to develop both small and large unit (e.g., onset and rime, morphemes, or even whole words) decoding strategies in parallel (Brown & Deavers, 1999; Goswami, Ziegler, Dalton, & Schneider, 2001, 2003; Ziegler & Goswami, 2005). However, it is not clear how orthographic transparency affects the reliance on small grain-size units in individuals with dyslexia. Despite a common core phonological deficit, there is evidence suggesting that the expression of dyslexia in different languages is affected by orthographic transparency (de Jong & van der Leij, 2003; Katzir, Shaul, Breznitz, & Wolf, 2004; Oren & Breznitz, 2005; Paulesu et al., 2001; Vellutino, Fletcher, Snowling, & Scanlon, 2004; Ziegler et al., 2003). Moreover, cross-linguistic studies typically compare between different populations, which differ not only in the orthographic transparency of their script but also in the phonological, morphological and grammatical structure of their spoken language, as well as cultural, educational and individual differences. Therefore, effects attributed to orthographic transparency may be confounded with these other variables. A primary deficit in phonological processing might hinder the ability to create well-specified orthographic word representations during reading acquisition (Perfetti, 2007; Share, 2008). These ideas are supported by behavioral studies showing that dyslexic readers are more sensitive to reduced word familiarity, frequency and imageability, especially for difficult-to-decode irregular words with inconsistent spelling-to-sound mapping (Bruck, 1992; Shaywitz & Shaywitz, 2003; Strain & Herdman, 1999).

Hebrew provides a unique opportunity to examine the effects of orthographic transparency and familiarity on reading in a within-language within-subject design. However, only one previous functional Magnetic Resonance Imaging (fMRI) study (Karni et al., 2005) had studied Hebrew readers with dyslexia. The current study uses fMRI to examine the interaction between orthographic transparency and familiarity on the neural mechanisms involved in Hebrew readers with dyslexia.

1.1. *Neural basis of dyslexia – deficit and compensation models*

Consistent with the idea of deficient phonological processing in dyslexia, neuroimaging studies with dyslexic children and adolescents in English typically show reduced activation in dorsal left temporo-parietal regions as compared to typical readers, including the supramarginal gyrus (SMG) and inferior parietal lobule (IPL), during tasks that require processing of printed words or phonological awareness (Hoeft et al., 2007; Landi, Mencl, Frost, Sandak, & Pugh, 2010; Raschle, Zuk, & Gaab, 2012; Shaywitz et al., 2002). Structural connectivity studies also showed reduced gray matter (Hoeft et al., 2007) and decreased white mater integrity in temporo-parietal regions in poor readers (Ben-Shachar, Dougherty, & Wandell, 2007; Klingberg et al., 2000; Odegard, Farris, Ring, McColl, & Black, 2009). The reduced activation for dyslexic readers in dorsal left temporo-parietal regions may suggest a specific deficit in the integration of orthographic and phonological information. However, adult dyslexic readers also show reduced activation in left angular gyrus (AG) and middle temporal gyrus (MTG), typically associated with semantic processing, in semantic reading related tasks (Shaywitz et al., 1998), which may reflect a secondary deficit in access to lexical-semantic processing (Lyon, Shaywitz, & Shaywitz, 2003; Perfetti, 2007, 2011; Pugh et al., 2010; Ziegler & Goswami, 2005). In addition, dyslexic readers show reduced activation in left ventral occipito-temporal (OT) cortex in tasks that require processing of printed words or phonological awareness (Brunswick, McCrory, Price, Frith, & Frith, 1999; Hoeft et al., 2007; Landi et al., 2010; Paulesu, Danelli, & Berlingeri, 2014; Raschle et al., 2012; Shaywitz et al., 1998, 2002), and lexical-semantic tasks (Christodoulou et al., 2014; Waldie, Haigh, Badzakova-Trajkov, Buckley, & Kirk, 2013). The reduced activation found for dyslexic readers in this region is often interpreted as reflecting deficient fluency and slow visual word recognition (McCandliss & Noble, 2003; Pugh et al., 2000).

In contrast to regions showing *reduced* activation in dyslexic readers, the left inferior frontal cortex typically shows *increased* activation during reading related tasks in dyslexic English readers (Brunswick et al., 1999; Christodoulou et al., 2014; Georgiewa et al., 2002; Hoeft et al., 2007; Shaywitz et al., 1998, 2002). This is commonly interpreted as reflecting stronger and more effortful reliance on pronunciation and sub-vocal articulation to use for phonological assembly during reading (Demonet et al., 1992). A number of studies that examined the neural correlates of dyslexia across development found that, in contrast to adult dyslexic readers, young dyslexic children do not show increased activation in left inferior frontal gyrus (IFG) (Booth, Bebko, Burman, & Bitan, 2007; Raschle et al., 2012; Richlan, Kronbichler, & Wimmer, 2011; Shaywitz et al., 2002), suggesting that it reflects a compensatory pathway that develops with reading experience.

1.2. *The effect of orthographic transparency on dyslexic readers*

There is a debate in the literature regarding the universality of the cognitive and neurobiological basis of dyslexia across languages. A large body of research suggests that dyslexic readers across all alphabetic Indo-European orthographies share the same atypical activation patterns found for dyslexics in English, described earlier (Diehl, Frost, Mencl, & Pugh, 2011; Paulesu et al., 2001; Pugh et al., 2010, 2000; Sandak, Mencl, Frost, & Pugh, 2004). In contrast, other studies suggest that the neurobiological marker of dyslexia is influenced by the specific orthography, and that differences in demands between orthographies must be taken into account (Castles &

Friedmann, 2014; Dehaene, 2014; Hadzibeganovic et al., 2010). For example, while dyslexic English readers show increased activation in left IFG compared to typical readers (Brunswick et al., 1999; Christodoulou et al., 2014; Hoeft et al., 2007; Shaywitz et al., 1998, 2002), dyslexic readers of more transparent orthographies such as Italian (Brambati et al., 2006) and German (Georgiewa et al., 1999; Richlan et al., 2010; Wimmer et al., 2010), show decreased activation in this region compared to typical readers. While many studies examined the manifestation of dyslexia in Indo-European orthographies, less is known about the neural basis of reading in dyslexic readers in Semitic languages. Given the vast cross-linguistic differences in spoken and written language it is important to examine whether similar deficient and compensatory neural mechanisms are evident in dyslexic Hebrew readers. More specifically, it is unclear how individuals with a phonological deficit cope with missing phonological information, as in Hebrew un-pointed script, or with a full but less familiar phonological information, as in Hebrew pointed script. The current study examines the effect of orthographic transparency on reading in this population.

1.3. The effect of orthographic familiarity on dyslexic readers

Studies that examined the effect of orthographic familiarity on dyslexic readers show mixed results. On the one hand, dyslexic children show reduced sensitivity to orthographic familiarity compared to typical readers within the left OT cortex, when presented with familiar and unfamiliar word-forms (van der Mark et al., 2009). On the other hand, both dyslexic and typical readers show sensitivity to words' familiarity in left IFG and superior temporal gyrus (STG) (Heim, Wehnelt, Grande, Huber, & Amunts, 2012; Pugh et al., 2008). However, the effect of orthographic familiarity in each group may be modulated by the orthographic transparency. In a relatively transparent orthography (German), both typical and dyslexic readers show increased activation in left IFG for less familiar words (Heim et al., 2012). In contrast, in a less transparent orthography (English), typical readers show increased activation, while dyslexic readers show decreased activation for less familiar words (Pugh et al., 2008).

The balance between orthographic transparency (a property of the written system) and familiarity (the interplay between the reader and the orthography) has been scarcely addressed in studies with dyslexic readers. The aim of the current study was to examine the effect of orthographic familiarity and its interaction with orthographic transparency on the brain of dyslexic readers.

1.4. Orthographic transparency and familiarity effects on dyslexic Hebrew readers

Hebrew has one script with two versions that differ in their orthographic transparency. The un-pointed opaque version includes mostly consonants graphemes, while vowel sounds are only partially represented by vowel letters. Moreover, vowel letters are ambiguous because they represent a consonant and one or more vowels. This creates an extensive phonological under-specification as well as pervasive homography (Bar-On, 2010). In contrast, the pointed, transparent version contains diacritic marks (in addition to consonants and vowel letters) which provide full representation of vowel sounds. This duality provides a unique opportunity to examine the effect of orthographic transparency on reading in a within-language within-subject design. However, it should also be noted that pointed words are mostly encountered during early years of reading acquisition, and are absent from most texts for skilled readers. Therefore, in the case of adult Hebrew readers the highly transparent script is also less frequently encountered and thus less familiar as compared to the un-pointed less transparent script (Weiss, Katzir, & Bitan, 2015a; for extended description).

A first attempt to examine the interplay between orthographic transparency and familiarity in dyslexic Hebrew readers with a phonological processing deficit was reported in our recent behavioral study (Weiss, Katzir, & Bitan, 2015b). Dyslexic readers were not only slower and less accurate than typical readers overall, but they also read pointed words (with diacritics that provide transparent but less familiar information) slower than un-pointed words, while typical readers did not show this effect. These results may suggest that dyslexic readers cannot harness the advantages of a transparent orthography, because of their phonological decoding deficit, or that they are more prone to interference by the low familiarity in pointed words, or both. However, the presence of the diacritics had an effect on the reading mechanism of typical readers as evident by the classic length effect (longer words were read slower and less accurately than short words), demonstrated only in pointed words. This length effect is consistent with previous studies showing a greater effect of word length in transparent orthographies (Cuetos & Suarez-Coalla, 2009; De Luca, Barca, Burani, & Zoccolotti, 2008; Ellis & Hooper, 2001; Hawelka, Gagl, & Wimmer, 2010; Marinus & de Jong, 2010), and may indicate that reading pointed words involves serial phonological assembly (Ziegler et al., 2003). In contrast to diacritic marks, vowel letters improved reading latency and accuracy in un-pointed words for both dyslexic and typical readers, suggesting that dyslexic Hebrew readers with phonological deficit actually may benefit from increased orthographic transparency when the representations are familiar.

Neuroimaging research can shed light on the brain function of dyslexic readers facing the unique demands of Hebrew. In one Event-Related Potentials (ERP) study that directly examined the role of diacritics with a lexical decision task in Hebrew, adult dyslexics showed smaller differences between pointed and un-pointed words, as compared to typical readers in ERP (N170) amplitudes in bilateral OT sites associated with early visual-perceptual stage of orthographic processing. The authors suggested that dyslexic readers failed to efficiently adjust to the demands of each script (Bar-Kochva & Breznitz, 2014). In a recent fMRI study with typical adult Hebrew readers (Weiss et al., 2015a), we found opposite effects of diacritics and vowel letters on activation in temporo-parietal regions associated with mapping orthography to phonology (left SMG, and left IPL). The increase in activation for diacritic marks (most transparent but less familiar) and the decrease in activation for vowel letters (familiar but not as transparent as diacritic marks) in these regions may suggest that the greater familiarity of vowel letters compared to diacritics overrides the effect of orthographic transparency for typical Hebrew readers. Vowel letters also reduced activation in regions associated with lexical and semantic processing (left pars orbitalis – Orb and pars triangularis – Tri, as well as left MTG and AG) in un-pointed words, suggesting a secondary effect of enhanced phonological information on semantic access.

1.5. *The current study*

In the current study we aimed to examine the effects of orthographic transparency and familiarity on the neurocognitive reading mechanisms in dyslexic Hebrew readers using fMRI. We used the same stimuli as in our recent behavioral study (Weiss et al., 2015b). The effect of orthographic transparency was examined by comparing brain activation of reading pointed and un-pointed words, and by comparing words with and without vowel letters. While vowel letters do not provide full phonological information like diacritic marks, they still increase orthographic transparency by providing partial phonological information. The effect of familiarity with the visual and orthographic representations is evident in the comparison of pointed words (less familiar for adult Hebrew readers) and un-pointed words (more familiar). To examine whether additional phonological information increases the reliance on assembled reading, we also manipulated the number of consonants, because a word length effect is a sensitive indicator of assembled reading (De Luca et al., 2008; Ellis & Hooper, 2001; Ellis et al., 2004).

We asked two general questions: *1) Is there neural evidence for a core phonological deficit and for compensatory mechanisms in dyslexic Hebrew readers?* To answer this question, we compared brain activation of dyslexic and typical readers in dorsal temporo-parietal, ventral OT and inferior frontal cortices that showed differential activation for dyslexic readers in previous studies (Kronbichler et al., 2006; Paulesu et al., 2001; Richlan et al., 2010). We predicted that dyslexic Hebrew readers, will show reduced activation in the left temporo-parietal junction (TPJ) and fusiform gyrus (FG). In aim to address the discrepancy in the literature regarding the left IFG (reduced or increased activation for dyslexic as compared to typical readers), we examined activation separately in different subregions within the left IFG, namely: pars opercularis (Oper), Tri, and Orb which are involved in different processes.

2) What is the effect of increasing orthographic transparency on the dyslexic reader's brain, and how does it interact with the familiarity of the graphemic representation? To answer these questions, we examined the effects of orthographic transparency and familiarity, separately in each group, in regions that were shown to be sensitive to these variables in typical readers (Weiss et al., 2015a). Given that diacritics interfere with reading speed in dyslexic readers (Weiss et al. 2015b), we predicted that in contrast to typical readers they would not be able to enhance activation in left TPJ for pointed words, due to their dysfunction in this region. However, dyslexic readers might compensate for the reduced familiarity of pointed words by enhancing the reliance on primary sensory, and/or semantic mechanisms. In contrast to diacritics, vowel letters had a facilitating effect in both typical and dyslexic readers (Weiss et al., 2015b). Hence, we predicted that dyslexic readers would show the same effect of vowel letters on brain activation as found for typical readers (Weiss et al., 2015a), namely, reduced activation in regions associated with phonological and lexical-semantic representations for words with as compared to without vowel letters.

2. Method

2.1. *Participants*

A group of 21 dyslexic readers was recruited through the student support services at universities and colleges in Israel. All participants in the research group were diagnosed as dyslexics in childhood. In addition, they were currently diagnosed as dyslexics by the university student support services, and matched the definition of 'compensated' dyslexics (Miller-Shaul, 2005). Ages ranged from 19:11 to 32:06 years ($M = 26$:10, standard deviation – $SD = 3$:05, nine males). The control group included 22 age matched typical readers of which 18 were included in the results reported in our former fMRI study (Weiss et al., 2015a). Four additional participants were recruited to the control group in this study to match groups by total number of participants and gender. The age range for the control group was from 22:03 to 33:07 years ($M = 28$:03, $SD = 2$:07, 11 males). All participants were native Hebrew speakers, right-handed, and displayed normal (or corrected to normal) vision in both eyes. None of them had a history of neurological, attention or psychiatric disorders. Inclusion criteria for the dyslexic readers group were both current and childhood diagnosis of dyslexia and a score lower than 1 SD below the average of the local norms (reported in Appendix A), in at least one of the two phonological tests: decoding (one minute pseudoword test; Shatil, 1997) and awareness (phoneme deletion test for pseudowords; Ben Dror & Shani, 1996). Same criterion was used in our former behavioral study (Weiss et al., 2015b). Means and SD of all measures for the two groups are presented in Table 1. Dyslexic readers' performed significantly worse than typical readers in all measures.

2.2. *Stimuli*

The stimuli in the current study is the same stimuli used in our former behavioral study (Weiss et al., 2015b) and consist of 192 Hebrew concrete nouns in four lists (48 words in each list) of two word lengths: three versus four consonants; and two vowel letter conditions: with or without a vowel letter (vowel letters included: yod, vav and he; all words were presented in their typical written form and vowel letters were not removed or inserted into these forms). All words were bi-syllabic, mono-morphemic and were matched for frequency across conditions, both in means and distribution. In order to avoid lexical ambiguity of both pointed and un-pointed word-forms, we avoided the inclusion of homographic words. As there is no available consensus corpus for written Hebrew frequency,

Table 1 – Means and SD of selection tests and other measures.

	Units of measure	Dyslexic readers (N = 21)	Typical readers (N = 22)	Sig.
Phoneme deletion test	Total time (sec)	177.23 (45.63)	84.62 (7.65)	$p < .001$
	Number of correct answers	15.19 (6.36)	23.72 (1.51)	$p < .001$
One minute pseudoword tests	Number of correct pseudowords per minute	27.04 (10.29)	60.45 (8.26)	$p < .001$
One minute word tests	Number of correct words per minute	60.04 (18.33)	95.18 (18.26)	$p < .001$

Note. SDs are given in parenthesis.

Table 2 – Examples of words for each experimental condition.

	Four consonants with vowel letter	Four consonants without vowel letter	Three consonants with vowel letter	Three consonants without vowel letter
With	סְנַפִּיר	אַרְנָב	תִּירָס	גֶּפֶן
diacritics	סנפיר	ארנב	תירס	גפן
Without	SNPIR	ARNV	TIRS	GFN
diacritics	/snapir/	/a'rnav/	/tiras/	/gefen/
	(fin)	(rabbit)	(corn)	(vine)
Word frequency				
Mean	3.19	3.35	3.41	3.34
SD	1.02	1.03	1.00	1.14
Range	(1.33–4.75)	(1.25–5)	(1.41–4.91)	(1.12–5)

our frequency ranking was based on subjective rating of 14 elementary school teachers on a 1–5 Likert scale, that represent a range of average to high frequency in adult texts (see Table 2).

2.3. *Experimental procedure*

Each trial began with a 200 msec presentation of a fixation cross followed by the presentation of the stimulus word for 1500 msec and then a blank screen for 2300 msec. Participants were required to read the word aloud as soon as it appears on the screen, and their responses and reaction times were monitored by an Magnetic Resonance Imaging (MRI) compatible microphone with noise cancellation (FOMRI™ III system, Optoacoustics Ltd.).

Stimuli were presented using E-Prime stimulus presentation software (v.2.0, Psychological Software Tools, Inc.). Pointed and un-pointed words were presented in separate runs to minimize interference which may arise from frequent shifting between versions. Half of the words in the list appeared first in their pointed version and half appeared first in their un-pointed version. Four runs of pointed words and four runs of un-pointed words appeared in alternating order, and the order was counter balanced across individuals. Stimuli from the current experiment were presented together with 56 words[1] from another experiment (Weiss, Katzir, & Bitan, in preparation) which were similar in length and frequency and appeared in both the pointed and un-pointed versions, but were not included in the analysis; 496 experimental trials were intermixed with 96 baseline trials in which the participants saw a string of asterisks and were required to say the word ‘pass’. Words from all experimental conditions and baseline trials were intermixed in an event-related design. Trial interval was jittered with 30% time of null and the sequence of trials was optimized using Optseq (Dale, 1999; http://surfer.nmr.mgh.harvard.edu/optseq/). The total of 592 trials were acquired in eight runs of 5:42 min. A practice list of 10 different words was presented to participants immediately prior to the first experimental run.

[1] The stimuli included Hebrew nouns with 2–3 syllables and 4–5 letters.

2.4. *fMRI data acquisition*

Images were acquired using a 3.0 T General Electric (GE) scanner with a standard head coil. The stimuli were projected onto a screen, and viewed through a mirror attached to the inside of the head coil. Participant's oral reading was monitored, to ensure their compliance with the task requirements. Functional images were acquired with a susceptibility weighted single-shot EPI (echo planar imaging) with BOLD (blood oxygenation level-dependent) with the following parameters: TE = 35 msec, flip angle = 78°, matrix size = 96×96, field of view = 20 cm, slice thickness = 3 mm + 1 mm gap, number of slices = 26 in a sequential ascending order, repetition time (TR) = 2000 msec. 171 images were acquired during each run. In addition, a high resolution, anatomical T1 weighted 3D structural images were acquired (AX SPGR, TR = 9.044 msec, echo time (TE) = 3.0504 msec, flip angle = 13°, matrix size = 256×256, field of view = 25.6 cm, slice thickness = 1 mm) using an identical orientation as the functional images. fMRI scans were performed in The Functional Brain Imaging Center, at the Tel-Aviv Sourasky Medical Center.

2.5. *fMRI data preprocessing and statistical analysis*

Data were analyzed using the Statistical Parametric Mapping toolbox for Matlab (SPM8 – Welcome Trust Centre for Neuroimaging, University College London, www.fil.ion.ucl.ac.uk/spm). The images were spatially realigned to the first volume in each run to correct for head movements. Average displacement in x, y or z dimensions across runs and across subjects is .8 mm (range = .1–3.5 mm). Sinc interpolation was used to minimize timing errors between slices (Henson, Buechel, Josephs, & Friston, 1999). The functional images were coregistered with the anatomical image, and normalized to the standard T1 template volume (MNI- Montreal Neurological Institute). The data were then smoothed with a 5-mm isotropic Gaussian kernel.

Statistical analyses at the first level were done separately for pointed and un-pointed words, in each participant using the General Linear Model (GLM) analysis for event-related designs. A high-pass filter with a cutoff period of 128 sec was applied. Movement parameters calculated during realignment were included as regressors of no interest. The model included two levels of vowel letters (with and without a vowel letter), and two levels of word length (three *vs* four consonants) as well as the baseline condition. These contrasts were taken in the first level analysis: pointed words > baseline, and un-pointed words > baseline. The contrast of each condition versus baseline, separately for pointed and un-pointed words, was carried into the second level group analysis. To avoid a possible effect of reduced brain response due to repetition of words across conditions (pointed and un-pointed), we conducted a preliminary analysis restricted to the first occurrence of each word. No differences were found between this analysis and the analysis with the two occurrences in the effects of experimental condition. Thus, we decided to include both occurrences in the analysis to increase statistical power. Activation maps for each group across all conditions are depicted for descriptive purpose at significance level of $p < .05$ corrected for multiple comparisons (Bonferroni), using a cluster extent threshold of $k \geq 50$ (see Fig. 1a).

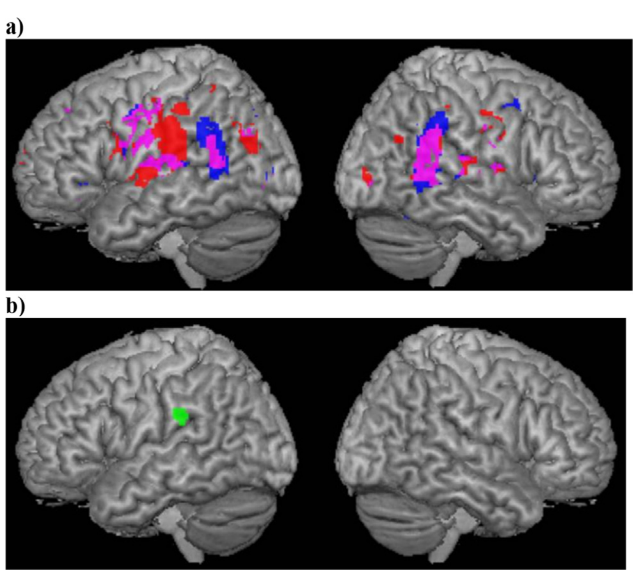

Fig. 1 – Activation maps across pointed and un-pointed words: a) Activation for typical readers (red), dyslexic readers (blue), and the overlap between them (violet). Threshold $p < .001$ uncorrected with cluster extent $k \geq 10$. b) Group differences in activation across other conditions. Threshold $p < .001$ uncorrected with cluster extent $k \geq 50$.

2.6. *Whole brain group analyses*

To compare between groups, whole brain analysis was conducted by means of the flexible factorial design with the factors: group and diacritics (using the first level contrasts: pointed words > baseline, and un-pointed words > baseline). Statistical maps comparing between groups across experimental conditions are depicted at significance level of $p < .001$ uncorrected for multiple comparisons, using a cluster extent threshold of $k \geq 50$ (see Fig. 1b).

2.7. *ROI analyses*

Regions of interest (ROI) were anatomically defined based on brain areas showing differential activation between typical and impaired visual word recognition in previous studies (Kronbichler et al., 2006; Paulesu et al., 2001; Richlan et al., 2010), and regions showing effects of orthographic transparency, familiarity and word length in typical readers (Weiss et al., 2015a). Ten specific anatomical regions of interest were defined in the left hemisphere based on the Automated Anatomical Labeling atlas (AAL) (Tzourio-Mazoyer et al., 2002): IFG including: 1) Oper, 2) Tri and 3) Orb; TPJ: including 4) SMG, 5) AG and 6) IPL; 7) MTG; 8) STG; 9) FG; and 10) Middle occipital gyrus (MOG). Changes in signal intensity during word reading were extracted using the MarsBaR toolbox for SPM (MARSeille Boîte À Région d'Intérêt, v.0.43 – Brett, Anton, Valabregue, & Poline, 2002). For each anatomical ROI we extracted the betas for each of eight experimental conditions (two levels of diacritics × two levels of vowel letters × two levels of word length) and the baseline. We then calculated the differences between each condition and the baseline's beta values. These difference values served as the dependent variable in the statistical analysis. Statistical analysis was done using IBM SPSS Statistics software (v. 19).

The statistical analysis was carried out in two ways: 1) *Across groups* – We examined whether dyslexic Hebrew readers show atypical activation in the same brain regions identified in other orthographies namely: left IFG (Christodoulou et al., 2014), TPJ (Hoeft et al., 2007), and FG (Raschle et al., 2012). For this purpose, we compared between groups in GLM repeated measures analyses conducted separately for each one of these larger cortical areas (three ROIs in IFG; three ROIs in TPJ, and one ROI in FG). This analysis was carried out with four within-subject factors: ROI (for IFG and TPJ), diacritics, vowel letters and length and with group as a between subject factor. We examined the sub-regions within left TPJ (SMG, IPL, AG) and left IFG (Oper, Tri, Orb), as studies with both typical and dyslexic readers indicate that each is associated with different functions (Binder, Desai, Graves, & Conant, 2009; Poldrack et al., 2001). To follow-up interaction with ROI, separate analyses within ROIs are presented with $p < .05$ corrected for the three ROIs (i.e., $p < .016$).

2) *Within each group* – The second analysis was conducted in order to examine the effect of diacritics, vowel letters and word length on dyslexic readers. We conducted separate GLM analyses within each group within each one of the 10 ROIs (SMG, IPL, AG, MTG, STG, FG, MOG, Oper, Tri and Orb). These analyses include three within-subject variables: diacritics,

vowel letters and word length. The results are reported with $p < .05$ corrected for 10 ROIs (i.e., $p < .005$).

3. Results

3.1. *Whole brain analysis*

The activation maps for each group across all conditions presented in Fig. 1a show mostly overlapping activation in frontal, temporal and temporo-parietal regions reading network. The whole brain repeated measures Analysis of variance (ANOVA) reveals activation differences between dyslexic and typical readers in left temporo-parietal regions across conditions (non-directional *F* test). In addition it reveals activation differences between pointed and un-pointed words in bilateral occipital and frontal regions across groups. No significant interaction was found between group and word types. The results of between group analyses are presented in Fig. 1b and Table 3.

3.2. *Between group ROI analysis*

Table 4 presents the results of the between groups analysis in left IFG, TPJ and FG, and follow-up analyses on the interactions with ROI or among experimental conditions (diacritics, vowel letters and length).

Fig. 2 shows significant main effects and interactions with group. Dyslexic readers show significant underactivation as compared to typical readers only in left SMG (see Fig. 2a). An

Table 3 – Whole brain differences between dyslexic and typical readers across conditions, and between pointed and un-pointed words across groups.

Contrast	Area	BA	H	Z score	Voxels	x	y	z
Typical readers > Dyslexic readers	SMG/IPL	40	L	3.78	50	−60	−32	28
Pointed words > Un-pointed words	MOG	18	R	4.80	115	34	−88	6
	MFG	9	R	4.31	78	34	−4	48
	MOG	18	L	4.28	66	−32	−88	10
	IFG/precentral g.	6	R	3.93	60	46	6	30
	Precentral g.	6	L	3.61	51	−44	−2	32
Un-pointed words > Pointed words	MOG/Lingual g./Cuneus	18	R	4.62	278	12	−92	12
	MOG/Lingual g./Cuneus	18	L	4.53	52	−14	−94	8
	Ant. Cingulate/SFG/MFG	32	L	4.51	339	−10	44	−2
Group × Word type	n.s							

Threshold $p < .001$ uncorrected with cluster extent $k \geq 50$. BA- Brodmann Area.

Table 4 – Between group analysis: significant main effects and interactions of experimental conditions, ROI and group in the large cortical areas.

ROI	Effect	dfn	dfd	F
L.IFG	ROI × Group	2	40	4.912*
	With vowel < Without vowel	1	41	30.453***
	Diacritics × Length	1	41	4.579*
	ROI × Diacritics × Length	2	40	5.986**
	ROI × Vowels	2	40	4.388*
L.Orb	With vowel < Without vowel	1	41	13.389***
L.Tri	With vowel < Without vowel	1	41	20.066***
L.Oper	With vowel < Without vowel	1	41	35.410***
	Diacritics × Length	1	41	10.075**
	Reversed length effect only in un-pointed words	1	41	8.722**
L.TPJ	ROI	2	40	5.538**
	With vowel < Without vowel	1	41	12.124***
	ROI × Diacritics	2	40	9.162***
	ROI × Vowels	2	40	5.607**
	ROI × Diacritics × Vowels	2	40	3.759*
	ROI × Length × Vowels × Group	2	40	5.003*
	ROI × Diacritics × Length × Vowels	2	40	4.087*
L.SMG	Typical readers > Dyslexic readers	1	41	8.260**
L.AG	With vowel < Without vowel	1	41	12.041***
	Diacritics × Vowels	1	41	8.687**
	With vowel < Without vowel only in un-pointed words	1	41	20.421***
L.IPL	Pointed words > Un-pointed words	1	41	10.678**
	With vowel < Without vowel	1	41	12.631***
	Diacritics × Length	1	41	6.924*
L.FG	Diacritics × Length	1	38	5.025*
	Length × Vowels	1	38	6.206*

*$p \leq .05$ for the larger cortical areas, or $p < .16$ for specific ROIs, **$p \leq .01$, ***$p \leq .001$. dfn- degrees of freedom in the numerator. dfd- degrees of freedom in the denominator.

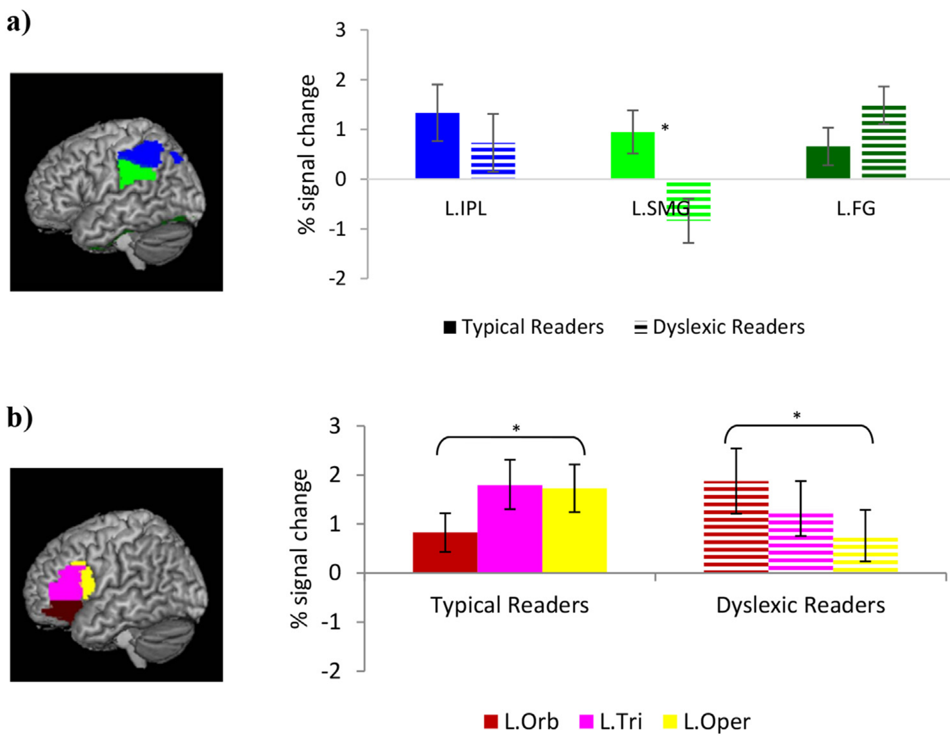

Fig. 2 – Effect of group. In ROIs showing group differences in other alphabetic orthographies. a) Underactivation for dyslexic as compared to typical readers in left SMG; b) Interaction between Group and ROI in left IFG. L.Orb (left Orb), L.Tri (left Tri) and L.Oper (left Oper). Significant effects are marked by asterisks (*$p \le .05$).

interaction between group and ROI was found in left IFG. None of the ROIs within IFG showed a significant difference between groups. However, while for typical readers activation in Orb was greater than in Oper, dyslexic readers showed the opposite pattern (see Fig. 2b). No region showed significant overactivation for dyslexic as compared to typical readers.

3.3. *Within group ROI analysis*

Table 5 and Figs. 3–5 present the results of planned comparisons within each group designed to test the sensitivity of dyslexic readers to diacritics, vowel letters and word length in the regions found for typical readers in our previous study (Weiss et al., 2015b). Results are presented at both an uncorrected threshold ($p < .05$) and following a correction for 10 ROIs ($p < .005$). For each ROI only variables that showed a significant effect (uncorrected $p < .05$) in at least one of the groups are presented in Table 5.

Fig. 3 shows effects of diacritics in the two groups. Typical readers showed increased activation for pointed as compared to un-pointed words in left IPL, SMG and MOG (see Fig. 3a), while dyslexic readers did not show a main effect of diacritics in any region (see Fig. 3b).

Fig. 4 shows the effect of word length in both groups. Typical readers showed more activation for long compared to short words in left STG, while in dyslexics this effect was found only in pointed words. Both typical and dyslexic readers showed a length effect in pointed words in left MOG (see Fig. 4).

Fig. 5 presents the regions showing an effect of vowel letters and an interaction of vowel letters and diacritics. Both typical and dyslexic readers showed decreased activation for words with vowel letters as compared to words without vowel letters in left IFG Oper and Tri, and left AG. Typical readers also showed this effect in left IPL (see Fig. 5a, b). Finally, both groups showed a reduced activation with vowel letters specifically for un-pointed words in left MTG (see Fig. 5c).

4. Discussion

Results from the current study indicate reduced activation for dyslexic as compared to typical readers in left SMG, consistent with a phonological deficit, as well as different patterns of activation within the left IFG. In contrast to typical readers, dyslexic readers did not show increased activation for diacritics in left TPJ regions, associated with mapping orthography to phonology. Nevertheless, both groups showed the facilitation effect of vowel letters on regions associated with lexical-semantic access.

4.1. *Differences between dyslexic and typical Hebrew readers*

Our results indicate that adult dyslexic Hebrew readers show reduced activation in the left SMG compared to controls. These results partially replicate findings from previous imaging studies in different alphabetic orthographies, indicating

Table 5 – Within group analyses: significant main effects and interactions of experimental conditions in each ROI and each group separately.

ROI	Effect	Typical readers			Dyslexic readers		
		dfn	dfd	F	dfn	dfd	F
L.IFG							
L.Orb	With vowel < Without vowel	1	21	7.553*	1	20	6.115*
	Diacritics × Vowels	1	21	9.113*			
L.Tri	With vowel < Without vowel	1	21	10.777**	1	20	9.637*
	Diacritics × Vowels	1	21	7.918*			
L.Oper	With vowel < Without vowel	1	21	24.807**	1	20	13.762**
	Diacritics × Vowels	1	21	5.381*			
	Diacritics × Length × Vowels	1	21	5.716*			
	Diacritics × Length				1	20	5.782*
L.TPJ							
L.SMG	Pointed words > Un-pointed words	1	21	6.042*			
	With vowel < Without vowel	1	21	6.626*			
	Length × Vowels				1	20	6.210*
L.AG	With vowel < Without vowel	1	21	4.608*	1	20	9.943**
	Diacritics × Vowels	1	21	6.306*			
	Length × Vowels	1	21	4.382*			
L.IPL	Pointed words > Un-pointed words	1	21	12.896**			
	With vowel < Without vowel	1	21	18.328**			
	Diacritics × Length	1	21	7.569*			
	Diacritics × Length × Vowels	1	21	5.408*			
L.MTG	With vowel < Without vowel	1	21	4.874*	1	20	7.006*
	Diacritics × Vowels	1	21	9.004*	1	20	11.230**
	With vowel < Without vowels only in un-pointed words	1	21	11.440**	1	20	4.359*
L.STG	Long words > Short words	1	21	11.768**			
	Diacritics × Length × Vowels	1	21	5.378*			
	Diacritics × Length				1	20	17.979**
	Long < Short only in pointed words				1	20	14.934**
L.FG	Diacritics × Length				1	19	4.958*
	Length × Vowels				1	19	7.972*
L.MOG	Pointed words > Un-pointed words	1	21	11.005**			
	Long words > Short words	1	21	12.107**	1	19	5.181*
	Diacritic × Length	1	21	14.758**	1	19	8.366*
	Long > Short only in pointed words	1	21	28.024**	1	19	12.567**

*$p \leq .05$, **$p \leq .005$ (correction for 10 ROIs). dfn- degrees of freedom in the numerator. dfd- degrees of freedom in the denominator.

a dysfunction of the left TPJ in dyslexic readers in reading related tasks (Diehl et al., 2011; Pugh et al., 2001, 2010). The left SMG is usually associated with phonological decoding and mapping of orthography to phonology (Booth et al., 2007; Demonet et al., 1992; Fiebach, Friederici, Müller, & Cramon, 2002; Graves, Binder, Desai, Conant, & Seidenberg, 2010; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Sandak et al., 2004; Xu et al., 2001). Thus, it is not surprising to find a reduced activation in this region for adult dyslexic Hebrew readers characterized by a phonological deficit. In contrast, we did not find the reduced activation in left FG associated with orthographic processing deficit found for dyslexic readers in English, French, Italian and German (Paulesu et al., 2001, 2014; Richlan, Kronbichler, & Wimmer, 2009; Richlan et al., 2011). The normal levels of activation in left FG for dyslexic readers in the current study may be a result of the fact that they are high-performing ("compensated") dyslexic readers who were admitted to higher education institutions. Despite their phonological deficit these individuals must have gained enough reading experience in their lifetime so that their specific deficit in the integration of orthography and phonology, did not expanded into a secondary orthographic deficit.

Finally, we found a significant difference between dyslexic and typical readers in the pattern of activation within IFG. Whereas typical readers showed more activation in IFG Oper than in Orb, dyslexic readers showed the opposite pattern. Given the association of IFG Oper with phonological segmentation (Burton, Small, & Blumstein, 2000; Hsieh, Gandour, Wong, & Hutchins, 2001; Poldrack et al., 2001) and of IFG Orb with lexical and semantic retrieval (Binder et al., 2009; Paulesu et al., 1997), these results are consistent with the idea that dyslexic readers with a phonological deficit are more likely to rely on lexical-semantic retrieval rather than phonological retrieval in reading. These results are in line with studies that found reduced activation specific to IFG Oper for dyslexic readers as compared to controls (Brambati et al., 2006; Georgiewa et al., 1999; Richlan et al., 2009; Wimmer et al., 2010). A recent meta-analysis reported that the reduced activation for dyslexic as compared to typical readers in left IFG

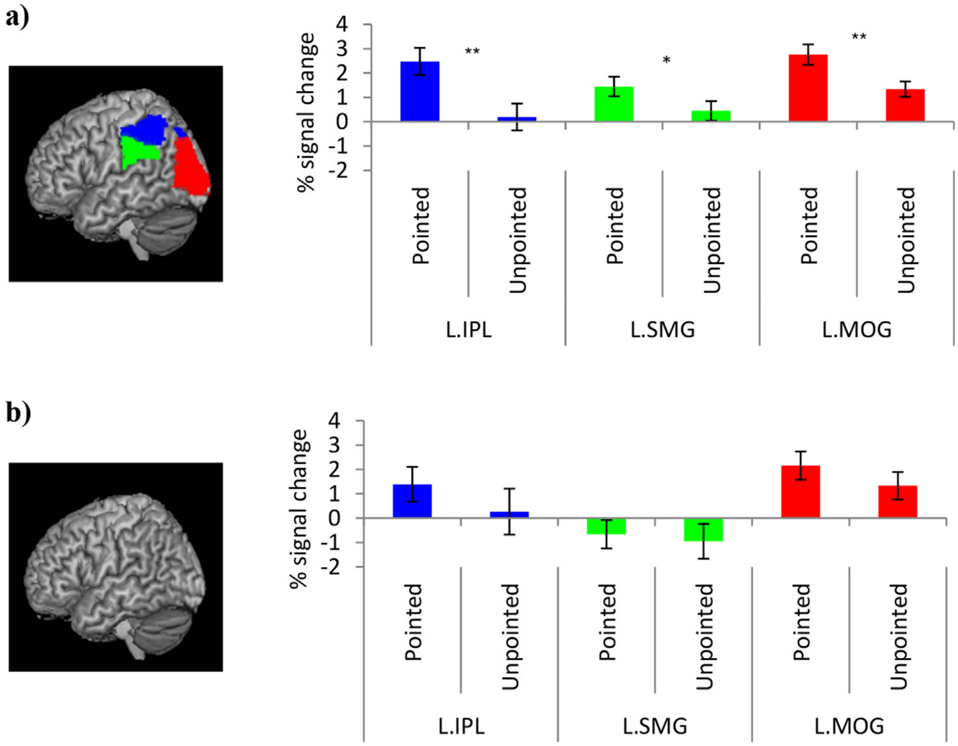

Fig. 3 – Effect of diacritics for typical readers (a) and dyslexic readers (b). ROIs showing main effect of diacritics in typical readers: L.IPL (left IPL), L.SMG (left SMG) and L.MOG (left MOG). Significant effects are marked by asterisks (*$p \leq .05$, **$p \leq .005$).

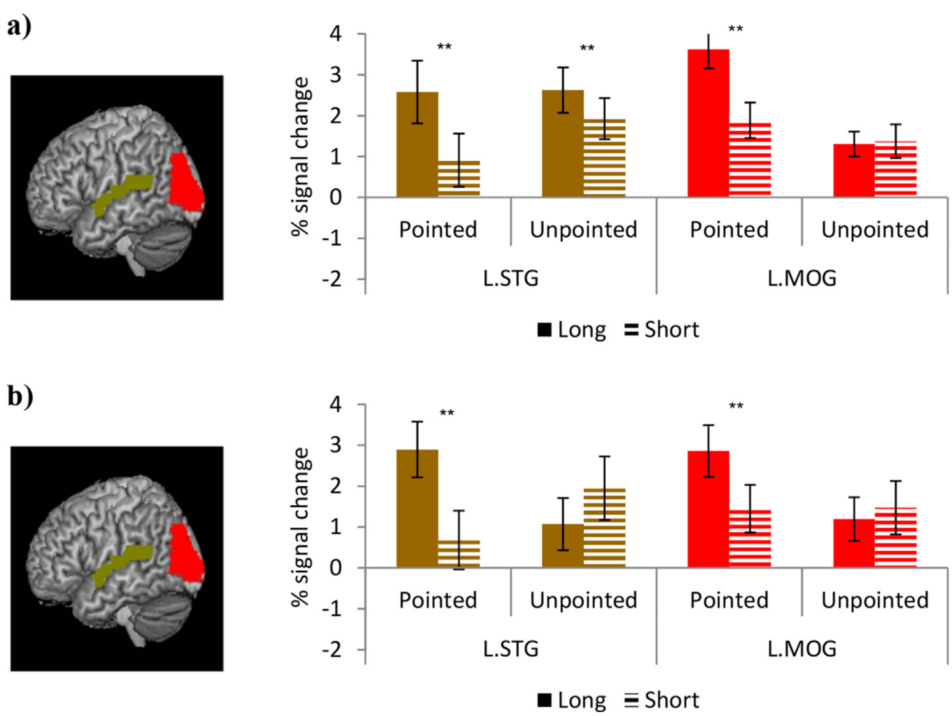

Fig. 4 – Effect of word length. ROIs showing interaction of word length and diacritics for typical readers (a) and for dyslexic readers (b). L.STG (left STG) and L.MOG (left MOG). Significant effects are marked by asterisks (*$p \leq .05$, **$p \leq .005$).

Oper is specific for adult readers (Paulesu et al., 2014). These results can also explain the inconsistency in the literature showing both increased (Brunswick et al., 1999; Christodoulou et al., 2014; Georgiewa et al., 2002; Hoeft et al., 2007; Shaywitz et al., 1998, 2002) or decreased (Brambati et al., 2006; Georgiewa et al., 1999; Richlan et al., 2010; Wimmer et al., 2010) activation in left IFG for dyslexic as compared to typical readers.

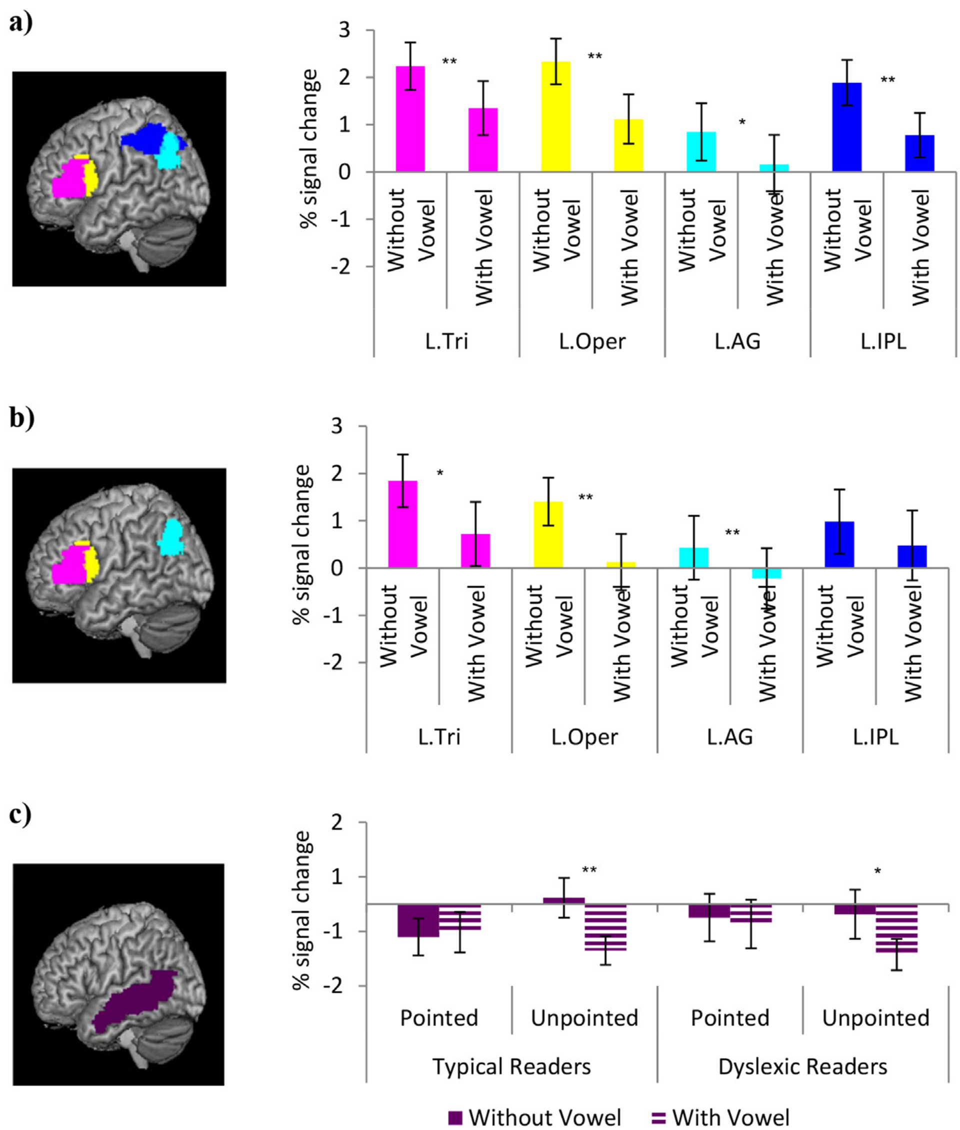

Fig. 5 – Effect of vowel letters. ROIs showing main effect of vowel letter in typical readers (a) and for dyslexic readers (b). L.Tri (left IFG Tri), L.Oper (left IFG Oper), L.AG (left AG), L.IPL (left IPL). Interaction of vowel letter and diacritics in typical and dyslexic readers (c) in L.MTG (left MTG). Significant effects are marked by asterisks (*$p \le .05$, **$p \le .005$).

4.2. *Effects of orthographic transparency and familiarity in dyslexic readers*

The main goal of this study was to examine the effects of orthographic transparency and familiarity on dyslexic Hebrew readers.

Temporo-parietal regions: Typical readers showed increased activation in left SMG and IPL for pointed words, which are both more transparent (and decodable) and less visually and orthographically familiar as compared to un-pointed words. The results of our behavioral study (Weiss et al., 2015b) suggest that typical adult Hebrew readers increased their reliance on assembly of small grain-size units when presented with pointed words, but they were efficient in assembled reading and it did not hinder their reading accuracy or fluency. Furthermore, the results for typical readers in the current study (see also Weiss et al., 2015a) show that in contrast to diacritics, increased orthographic transparency in the form of vowel letters, which do not compromise visual and orthographic familiarity, lead to *reduced* activation in left IPL, suggesting that the increased transparency in the form of vowel letters facilitated phonological processing and ortho–phono mapping, or disengaged from this process. Finally, in typical readers the presence of vowel letters also decreased activation in left AG, associated with mapping of orthography to semantics (Binder et al., 2009). These results, of reduced activation in left IPL and AG in the presence of vowel letters, together with the behavioral findings that vowel letters improved reading latency and accuracy (Weiss et al., 2015b), suggest that the presence of vowel letter reduced the effort on word recognition. The facilitative effect of vowel letters on reading latency may be due to its transparency, or alternatively due to reduced orthographic competition. We found in our previous behavioral study with the same stimuli, that words with more letters (either a consonant or a vowel letter) have smaller orthographic neighborhoods (Weiss et al., 2015b). It should be noted that this confound is inherent to the manipulations, since the additional letter restricts the number of potentially similar words (Baayen, Piepenbrock, & van, 1993; Norris & Kinoshita, 2012), and it does not depend on the specific stimuli selected for the study.

In contrast to typical readers, dyslexic readers did not show significant effects of diacritics or vowel letters in left SMG and IPL. The lack of significant effects in these regions together with the reduced activation in left SMG in dyslexic compared to typical readers are in line with previous findings showing dysfunction of left TPJ in dyslexic readers across languages (Diehl et al., 2011; Pugh et al., 2001, 2010). Our results further suggest that the dysfunction in these regions is associated with deficient decoding of small grain-size units. These results can explain the finding of slower reading of pointed compared to un-pointed words in dyslexic readers (Weiss et al., 2015b) by showing that dyslexic readers could not take advantage of the increased transparency in pointed words because they could not recruit left IPL and SMG and rely on mapping of small grain-size units. Nevertheless, dyslexic readers showed intact function in left AG, evident in reduced activation in left AG in the presence of vowel letters. This finding is in line with the behavioral facilitation of vowel letters found for both dyslexic as typical readers (Weiss et al., 2015b). One way in which vowel letters can facilitate reading without relying on decoding of small grain-size units is by increasing the number of letters in the word, thus reducing the number of orthographic competitors (Weiss et al., 2015b).

IFG: Both typical and dyslexic readers showed decreased activation in the presence of vowel letters in left IFG Oper and Tri, suggesting that the increased transparency lead to easier lexical retrieval and phonological processing. This is consistent with our behavioral results (Weiss et al., 2015b) showing that vowel letters facilitate reading of un-pointed words for both dyslexic and typical readers. These results are also in line with results from adult dyslexic readers in German, showing decreased activation in left IFG Oper with decreasing demands on orthographic processing (Heim et al., 2012), and may reflect an easier access to lexical and sublexical phonological output representations in the presence of vowel letters.

Visual and auditory processing regions: The presence of diacritic marks also affects lower level visual and auditory representations evident in changes in activation in left MOG and left STG. Dyslexic readers showed an interaction between diacritics and word length (the number of consonants in the word) in these regions, with increased activation for longer words only when they are presented with diacritics. This finding is consistent with our behavioral findings (Weiss et al., 2015b) showing slower reading of long words, only when they are pointed. These findings suggest that dyslexic readers were indeed sensitive to the reduced visual and orthographic familiarity inflicted by the presentation of diacritics, and this resulted in applying more segmental analysis to pointed words in lower level visual and auditory perceptual processing, despite the fact that they did not recruit the left IPL and SMG associated with mapping orthography to phonology when reading pointed words.

MTG: Finally, for both dyslexic and typical readers, vowel letters decreased activation in left MTG only for un-pointed words. This interaction between vowel letters and diacritics is in line with findings from our behavioral study, showing that vowel letters reduce reaction times only for reading un-pointed words for both typical and dyslexic readers (Weiss et al., 2015b). The association of left MTG with semantic processing (Binder et al., 2009; Fiebach et al., 2002; Fiez, 1997; Graves et al., 2010; Jobard et al., 2003; Kircher, Sass, Sachs, & Krach, 2009; Paulesu et al., 1997) suggests that only in the absence of diacritic marks the presence of vowel letters facilitate the lexical and semantic access for both typical and dyslexic readers.

5. Conclusions

Two main conclusions arise from the results of the current study. First, the reading deficit in dyslexic readers in our study can be explained by a dysfunction in parts of left TPJ (specifically, SMG and IPL), indicating deficient phonological processing and mapping of orthography to phonology and especially in decoding of small grain-size units. However, we did not find evidence in the brain for any secondary deficit in orthographic or lexical access as suggested by the lexical quality hypothesis (Perfetti, 2007). This may be due to the fact that our sample only includes "compensated" dyslexic readers. The dyslexic readers in our study seem to compensate for their reduced phonological decoding efficiency with increased reliance on lexical-semantic retrieval as evident by the pattern within IFG (they showed more activation in left IFG Orb, associated with lexical retrieval as compare to Oper, associated with phonological segmentation).

Second, while typical readers can compensate for the reduced visual and orthographic familiarity of pointed words with increased reliance on decoding of smaller units, dyslexic readers cannot, and therefore the cost for them is higher, as evident also by their slower reading times of pointed versus un-pointed words (Weiss et al., 2015b). However, when additional orthographic and phonological information is provided by vowel letters, without reducing familiarity, dyslexic readers, like typical readers, take advantage of this information, as evident by reduced load on regions involved in lexico-semantic access and improved reading latency and accuracy in un-pointed words for both dyslexic and typical readers (Weiss et al., 2015b). Altogether these results suggest that reading theories that focus solely on the effect of the transparency of the orthography, and do not take into account other factors such as familiarity, fail to describe the full picture of reading and reading impairment in different orthographies.

Acknowledgments

This work was supported by the Israel Science Foundation under grant 1142/11 to Bitan and Katzir; and NetWords under grant 09-RNP-089 to Weiss.

Appendix A. Local norms

	Units of measure	N	Mean (SD)	Criteria of 1 SD below average
One minute word tests	Number of correct words per minute	191	106.49 (18.41)	<88 correct words
One minute pseudoword tests	Number of correct pseudowords per minute	191	61.04 (14.146)	<46.89 correct pseudowords

REFERENCES

Baayen, R. H., Piepenbrock, R., & van, H. R. (1993). *The {CELEX} lexical data base on {CD-ROM}*.

Bar-Kochva, I., & Breznitz, Z. (2014). Reading scripts that differ in orthographic transparency: A within-participant-and-language investigation of underlying skills. *Journal of Experimental Child Psychology, 121*, 12–27.

Bar-On, A. (2010). *The role of linguistic knowledge in learning to read non-voweled Hebrew*. Israel: Tel Aviv University.

Ben Dror, I., & Shani, M. (1996). *Phoneme recognition test for words and pseudowords* (Unpublished Test).

Ben-Shachar, M., Dougherty, R. F., & Wandell, B. A. (2007). White matter pathways in reading. *Cognitive Neuroscience, 17*(2), 258–270. http://doi.org/10.1016/j.conb.2007.03.006.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex (New York, N.Y.: 1991), 19*(12), 2767–2796. http://doi.org/10.1093/cercor/bhp055.

Booth, J. R., Bebko, G., Burman, D. D., & Bitan, T. (2007). Children with reading disorder show modality independent brain abnormalities during semantic tasks. *Neuropsychologia, 45*(4), 775–783. http://doi.org/10.1016/j.neuropsychologia.2006.08.015.

Brambati, S. M., Termine, C., Ruffino, M., Danna, M., Lanzi, G., Stella, G., et al. (2006). Neuropsychological deficits and neural dysfunction in familial dyslexia. *Brain Research, 1113*(1), 174–185.

Brett, M., Anton, J. L., Valabregue, R., & Poline, J. B. (2002). Region of interest analysis using the MarsBar toolbox for SPM 99. *NeuroImage, 16*, S497.

Brown, G. D. A., & Deavers, R. P. (1999). Units of analysis in nonword reading: Evidence from children and adults. *Journal of Experimental Child Psychology, 73*(3), 208–242.

Bruck, M. (1992). Persistence of dyslexics' phonological awareness deficits. *Developmental Psychology, 28*(5), 874.

Brunswick, N., McCrory, E., Price, C. J., Frith, C. D., & Frith, U. (1999). Explicit and implicit processing of words and pseudowords by adult developmental dyslexics: A search for Wernicke's Wortschatz? *Brain : A Journal of Neurology, 122*(Pt 10), 1901–1917.

Burton, M., Small, S., & Blumstein, S. (2000). The role of segmentation in phonological processing: An fMRI investigation. *Journal of Cognitive Neuroscience, 12*(4), 679–690.

Castles, A., Bates, T., & Coltheart, M. (2006). John Marshall and the developmental dyslexias. *Aphasiology, 20*(9–11), 871–892. http://doi.org/10.1080/02687030600738952.

Castles, A., & Coltheart, M. (1993). Varieties of developmental dyslexia. *Cognition, 47*(2), 149–180. http://doi.org/10.1016/0010-0277(93)90003-E.

Castles, A., & Friedmann, N. (2014). Developmental dyslexia and the phonological deficit hypothesis. *Mind & Language, 29*(3), 270–285.

Christodoulou, J. A., Del Tufo, S. N., Lymberis, J., Saxler, P. K., Ghosh, S. S., Triantafyllou, C., et al. (2014). Brain bases of reading fluency in typical reading and impaired fluency in dyslexia. *PloS One, 9*(7), e100552.

Cuetos, F., & Suarez-Coalla, P. (2009). From grapheme to word in reading acquisition in Spanish. *Applied Psycholinguistics, 30*(04), 583–601.

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping, 8*(2–3), 109–114.

De Luca, M., Barca, L., Burani, C., & Zoccolotti, P. (2008). The effect of word length and other sublexical, lexical, and semantic variables on developmental reading deficits. *Cognitive and Behavioral Neurology : Official Journal of the Society for Behavioral and Cognitive Neurology, 21*(4), 227.

Dehaene, S. (2014). Reading in the brain revised and extended: Response to comments. *Mind & Language, 29*(3), 320–335.

Demonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., et al. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain, 115*(6), 1753–1768.

Diehl, J. J., Frost, S. J., Mencl, W. E., & Pugh, K. R. (2011). Neuroimaging and the phonological deficit hypothesis. In *Explaining individual differences in reading: Theory and evidence* (p. 217) (chapter 11).

Ellis, N. C., & Hooper, A. M. (2001). Why learning to read is easier in Welsh than in English: Orthographic transparency effects evinced with frequency-matched tests. *Applied Psycholinguistics, 22*(4), 571–599.

Ellis, N. C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V. H. P., Polyzoe, N., et al. (2004). The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. *Reading Research Quarterly, 39*(4), 438–468.

Fiebach, C., Friederici, A., Müller, K., & Cramon, D. von (2002). fMRI evidence for dual routes to the mental lexicon in visual word recognition. *Journal of Cognitive Neuroscience, 14*(1), 11–23.

Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping, 5*(2), 79–83.

Georgiewa, P., Rzanny, R., Gaser, C., Gerhard, U. J., Vieweg, U., Freesmeyer, D., et al. (2002). Phonological processing in dyslexic children: A study combining functional imaging and event related potentials. *Neuroscience Letters, 318*(1), 5–8.

Georgiewa, P., Rzanny, R., Hopf, J. M., Knab, R., Glauche, V., Kaiser, W. A., et al. (1999). fMRI during word processing in dyslexic and normal reading children. *NeuroReport, 10*(16), 3459.

Goswami, U., Ziegler, J. C., Dalton, L., & Schneider, W. (2001). Pseudohomophone effects and phonological recoding procedures in reading development in English and German. *Journal of Memory and Language, 45*(4), 648–664.

Goswami, U., Ziegler, J. C., Dalton, L., & Schneider, W. (2003). Nonword reading across orthographies: How flexible is the choice of reading units? *Applied Psycholinguistics, 24*(02), 235–247.

Graves, W. W., Binder, J. R., Desai, R. H., Conant, L. L., & Seidenberg, M. S. (2010). Neural correlates of implicit and explicit combinatorial semantic processing. *NeuroImage, 53*(2), 638–646.

Hadzibeganovic, T., van den Noort, M., Bosch, P., Perc, M., van Kralingen, R., Mondt, K., et al. (2010). Cross-linguistic neuroimaging and dyslexia: A critical view. *Cortex, 46*(10), 1312.

Hawelka, S., Gagl, B., & Wimmer, H. (2010). A dual-route perspective on eye movements of dyslexic readers. *Cognition, 115*(3), 367–379.

Heim, S., Wehnelt, A., Grande, M., Huber, W., & Amunts, K. (2012). Effects of lexicality and word frequency on brain activation in dyslexic readers. *Brain and Language*. http://doi.org/10.1016/j.bandl.2011.12.005.

Henson, R. N. A., Buechel, C., Josephs, O., & Friston, K. J. (1999). The slice-timing problem in event-related fMRI. *NeuroImage, 9*, 125.

Hoeft, F., Meyler, A., Hernandez, A., Juel, C., Taylor-Hill, H., Martindale, J. L., et al. (2007). Functional and morphometric brain dissociation between dyslexia and reading ability. *Proceedings of the National Academy of Sciences, 104*(10), 4234–4239.

Hsieh, L., Gandour, J., Wong, D., & Hutchins, G. D. (2001). Functional heterogeneity of inferior frontal gyrus is shaped by linguistic experience. *Brain and Language, 76*(3), 227–252.

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A metanalysis of 35 neuroimaging studies. *NeuroImage, 20*(2), 693–712.

de Jong, P. F., & van der Leij, A. (2003). Developmental changes in the manifestation of a phonological deficit in dyslexic children learning to read a regular orthography. *Journal of Educational Psychology, 95*(1), 22.

Karni, A., Morocz, I. A., Bitan, T., Shaul, S., Kushnir, T., & Breznitz, Z. (2005). An fMRI study of the differential effects of word presentation rates (reading acceleration) on dyslexic readers' brain activity patterns. *Journal of Neurolinguistics, 18*(2), 197–219.

Katzir, T., Christodoulou, J. A., & Chang, B. (2016). The neurobiological basis of reading fluency. In *Reading fluency* (pp. 11–23). Springer International Publishing.

Katzir, T., Misra, M., & Poldrack, R. A. (2005). Imaging phonology without print: Assessing the neural correlates of phonemic awareness using fMRI. *NeuroImage, 27*(1), 106–115.

Katzir, T., Shaul, S., Breznitz, Z., & Wolf, M. (2004). The universal and the unique in dyslexia: A cross-linguistic investigation of reading and reading fluency in Hebrew-and English-speaking children with reading disorders. *Reading and Writing, 17*(7), 739–768.

Kircher, T., Sass, K., Sachs, O., & Krach, S. (2009). Priming words with pictures: Neural correlates of semantic associations in a cross-modal priming task using fMRI. *Human Brain Mapping, 30*(12), 4116–4128.

Klingberg, T., Hedehus, M., Temple, E., Salz, T., Gabrieli, J. D. E., Moseley, M. E., et al. (2000). Microstructure of temporo-parietal white matter as a basis for reading ability: Evidence from diffusion tensor magnetic resonance imaging. *Neuron, 25*(2), 493–500.

Kronbichler, M., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., & Wimmer, H. (2006). Evidence for a dysfunction of left posterior reading areas in German dyslexic readers. *Neuropsychologia, 44*(10), 1822–1832.

Landi, N., Mencl, W. E., Frost, S. J., Sandak, R., & Pugh, K. R. (2010). An fMRI study of multimodal semantic and phonological processing in reading disabled adolescents. *Annals of Dyslexia, 60*(1), 102–121. http://doi.org/10.1007/s11881-009-0029-6.

Lyon, G. R., Shaywitz, S. E., & Shaywitz, B. A. (2003). Defining dyslexia, comorbidity, teachers' knowledge of language and reading: A definition of dyslexia. *Annals of Dyslexia, 3*(1), 1–14.

Manis, F. R., Seidenberg, M. S., Doi, L. M., McBride-Chang, C., & Petersen, A. (1996). On the bases of two subtypes of development dyslexia. *Cognition, 58*(2), 157–195.

Marinus, E., & de Jong, P. F. (2010). Variability in the word-reading performance of dyslexic readers: Effects of letter length, phoneme length and digraph presence. *Cortex, 46*(10), 1259–1271.

van der Mark, S., Bucher, K., Maurer, U., Schulz, E., Brem, S., Buckelmüller, J., et al. (2009). Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. *NeuroImage, 47*(4), 1940–1949. http://doi.org/10.1016/j.neuroimage.2009.05.021.

McCandliss, B. D., & Noble, K. G. (2003). The development of reading impairment: A cognitive neuroscience model. *Mental Retardation and Developmental Disabilities Research Reviews, 9*(3), 196–205.

Miller-Shaul, S. (2005). The characteristics of young and adult dyslexics readers on reading and reading related cognitive tasks as compared to normal readers. *Dyslexia, 11*(2), 132–151.

Norris, D., & Kinoshita, S. (2012). Reading through a noisy channel: Why there's nothing special about the perception of orthography. *Psychological Review, 119*(3), 517.

Odegard, T. N., Farris, E. A., Ring, J., McColl, R., & Black, J. (2009). Brain connectivity in non-reading impaired children and children diagnosed with developmental dyslexia. *Neuropsychologia, 47*(8), 1972–1977.

Oren, R., & Breznitz, Z. (2005). Reading processes in L1 and L2 among dyslexic as compared to regular bilingual readers: Behavioral and electrophysiological evidence. *Journal of Neurolinguistics, 18*(2), 127–151.

Paulesu, E., Danelli, L., & Berlingeri, M. (2014). Reading the dyslexic brain: Multiple dysfunctional routes revealed by a new meta-analysis of PET and fMRI activation studies. *Frontiers in Human Neuroscience, 8*.

Paulesu, E., Démonet, J. F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., et al. (2001). Dyslexia: Cultural diversity and biological unity. *Science, 291*(5511), 2165.

Paulesu, E., Goldacre, B., Scifo, P., Cappa, S. F., Gilardi, M. C., Castiglioni, I., et al. (1997). Functional heterogeneity of left inferior frontal cortex as revealed by fMRI. *NeuroReport, 8*(8), 2011–2016.

Perfetti, C. A. (2007). Reading ability: Lexical quality to comprehension. *Scientific Studies of Reading, 11*(4), 1–27.

Perfetti, C. A. (2011). Phonology is critical in reading – But a phonological deficit is not the only source of low reading skill.

Poldrack, R. A., Temple, E., Protopapas, A., Nagarajan, S., Tallal, P., Merzenich, M., et al. (2001). Relations between the neural bases of dynamic auditory processing and phonological processing: Evidence from fMRI. *Journal of Cognitive Neuroscience, 13*(5), 687–697.

Pugh, K., Frost, S. J., Sandak, R., Landi, N., Moore, D., Della Porta, G., et al. (2010). Mapping the word reading circuitry in skilled and disabled readers. In *The Neural Basis of Reading* (pp. 281–305).

Pugh, K., Frost, S. J., Sandak, R., Landi, N., Rueckl, J. G., Constable, R. T., et al. (2008). Effects of stimulus difficulty and repetition on printed word identification: An fMRI comparison of nonimpaired and reading-disabled adolescent cohorts. *Journal of Cognitive Neuroscience, 20*(7), 1146–1160.

Pugh, K., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., et al. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews, 6*(3), 207–213.

Pugh, K., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., et al. (2001). Neurobiological studies of reading and reading disability. *Journal of Communication Disorders, 34*(6), 479–492.

Raschle, N. M., Zuk, J., & Gaab, N. (2012). Functional characteristics of developmental dyslexia in left-hemispheric posterior brain regions predate reading onset. *Proceedings of the National Academy of Sciences of the United States of America, 109*(6), 2156–2161. http://doi.org/10.1073/pnas.1107721109.

Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*(10), 3299–3308.

Richlan, F., Kronbichler, M., & Wimmer, H. (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *NeuroImage, 56*(3), 1735–1742. http://doi.org/10.1016/j.neuroimage.2011.02.040.

Richlan, F., Sturm, D., Schurz, M., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A common left occipito-temporal dysfunction in developmental dyslexia and acquired letter-by-letter reading? *PloS One, 5*(8), e12073.

Sandak, R., Mencl, W. E., Frost, S. J., & Pugh, K. R. (2004). The neurobiological basis of skilled and impaired reading: Recent findings and new directions. *Scientific Studies of Reading, 8*(3), 273–292.

Share, D. L. (2008). Orthographic learning, phonological recoding, and self-teaching. *Advances in Child Development and Behavior, 36*, 31–82.

Shatil, E. (1997). *One-minute test for pseudowords* (Unpublished test). Haifa: University of Haifa.

Shaywitz, S. E., & Shaywitz, B. A. (2003). The science of reading and dyslexia. *Journal of AAPOS : The Official Publication of the American Association for Pediatric Ophthalmology and Strabismus/American Association for Pediatric Ophthalmology and Strabismus, 7*(3), 158–166. http://doi.org/10.1016/mpa.2003.S1091853103000028.

Shaywitz, S. E., Shaywitz, B. A., Pugh, K., Fulbright, R., Constable, R., Mencl, W., et al. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences of the United States of America, 95*(5), 2636.

Shaywitz, B. A., Shaywitz, S. E., Pugh, K., Mencl, W., Fulbright, R. K., Skudlarski, P., et al. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biological Psychiatry, 52*(2), 101–110.

Stanovich, K. E. (1988). Explaining the differences between the dyslexic and the garden-variety poor reader: The phonological-core variable-difference model. *Journal of Learning Disabilities, 21*(10), 590–604.

Strain, E., & Herdman, C. M. (1999). Imageability effects in word naming: An individual differences analysis. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 53*(4), 347.

Torgesen, J. K., Wagner, R. K., & Rashotte, C. A. (1994). Longitudinal studies of phonological processing and reading. *Journal of Learning Disabilities, 27*(5), 276–286.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage, 15*(1), 273–289.

Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): What have we learned in the past four decades? *Journal of Child Psychology and Psychiatry, 45*(1), 2–40.

Waldie, K. E., Haigh, C. E., Badzakova-Trajkov, G., Buckley, J., & Kirk, I. J. (2013). Reading the wrong way with the right hemisphere. *Brain Sciences, 3*(3), 1060–1075.

Weiss, Y., Katzir, T., & Bitan, T. (2015a). Many ways to read your vowels—Neural processing of diacritics and vowel letters in Hebrew. *NeuroImage, 121*, 10–19.

Weiss, Y., Katzir, T., & Bitan, T. (2015b). The effects of orthographic transparency and familiarity on reading Hebrew words in adults with and without dyslexia. *Annals of Dyslexia*, 1–19.

Weiss, Y. Katzir T. & Bitan, T. Effects of orthographic transparency and morphological complexity on brain of typical and dyslexic adults Hebrew readers. (in preparation).

Wimmer, H., Schurz, M., Sturm, D., Richlan, F., Klackl, J., Kronbichler, M., et al. (2010). A dual-route perspective on poor reading in a regular orthography: Evidence from phonological and orthographic lexical decisions. *Cognitive Neuropsychology, 25*(5), 653–676. http://doi.org/10.1080/02643290802221404.

Wolf, M., & Bowers, P. G. (1999). The double-deficit hypothesis for the developmental dyslexias. *Journal of Educational Psychology, 91*(3), 415.

Wolf, M., & Kennedy, R. (2003). How the origins of written language instruct us to teach: A response to Steven Strauss. *Educational Researcher*, 26–30.

Xu, B., Grafman, J., Gaillard, W. D., Ishii, K., Vega-Bermudez, F., Pietrini, P., et al. (2001). Conjoint and extended neural networks for the computation of speech codes: The neural basis of selective impairment in reading words and pseudowords. *Cerebral Cortex, 11*(3), 267–277.

Ziegler, J. C., & Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: A psycholinguistic grain size theory. *Psychological Bulletin, 131*(1), 3.

Ziegler, J. C., Perry, C., Ma-Wyatt, A., Ladner, D., & Schulte-Körne, G. (2003). Developmental dyslexia in different languages: Language-specific or universal? *Journal of Experimental Child Psychology, 86*(3), 169–193.

Zoccolotti, P., & Friedmann, N. (2010). From dyslexia to dyslexias, from dysgraphia to dysgraphias, from a cause to causes: A look at current research on developmental dyslexia and dysgraphia. *Cortex, 46*, 1211–1215.