NeuroImage 121 (2015) 10–19

Contents lists available at ScienceDirect

NeuroImage

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

Many ways to read your vowels—Neural processing of diacritics and vowel letters in Hebrew

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

[a] Department of Learning Disabilities, The E.J. Safra Brain Research Center for the Study of Learning Disabilities, University of Haifa, Haifa, Israel
[b] Psychology Department, University of Haifa, Haifa, Israel
[c] Department of Speech Pathology, University of Toronto, Canada

ARTICLE INFO

Article history:
Received 16 July 2014
Accepted 8 July 2015
Available online 15 July 2015

Keywords:
fMRI
Reading
Familiarity
Word length
Diacritics
Inferior parietal lobule

ABSTRACT

The current study examined the effect of orthographic transparency and familiarity on brain mechanisms involved in word recognition in adult Hebrew readers. We compared the effects of diacritics that provide transparent but less familiar information and vowel letters that increase orthographic transparency without compromising familiarity. Brain activation was measured in 18 adults during oral reading of single words, while manipulating the presence of diacritic marks, the presence of a vowel letter, and word length (3 vs. 4 consonants). We found opposite effects of diacritics and vowel letters on temporo-parietal regions associated with mapping orthography to phonology. The increase in activation for diacritic marks and the decrease in activation for vowel letters in these regions suggest that the greater familiarity of vowel letters compared to diacritics overrides the effect of orthographic transparency. Vowel letters also reduced activation in regions associated with semantic processing in unpointed words, and were thus distinct from the effect of an additional consonant. Altogether the results suggest that both orthographic transparency and familiarity contribute to word recognition.

Introduction

Writing systems represent units of spoken language, and thus are structured so that they optimally represent the languages' phonological spaces, and their mapping into semantic meanings (Frost, 2012). It is customary to characterize writing systems according to their orthographic transparency. In transparent orthographies, such as German or Spanish, the grapheme to phoneme correspondence is consistent, while in opaque orthographies, such as English or French, the grapheme to phoneme correspondence is less consistent.

The effects of orthographic transparency and the role of phonology in word recognition

There is a debate in the literature regarding whether phonological information mediates access to the mental visual word lexicon for adult readers. The Orthographic Depth Hypothesis (Katz and Frost, 1992), inspired by the Dual Route Model (Coltheart et al., 2001), suggests that readers rely on one of two routes for reading, depending on the demands of the specific orthography. In more transparent orthographies readers access to words' meaning through its phonology, by assembled (letter by letter) reading. In opaque orthographies, access through phonology is not obligatory and meaning can be accessed directly by decoding of large orthographic units (whole-word) (Katz and Frost, 1992).

In contrast, according to connectionist models (McClelland and Rumelhart, 1981; Seidenberg and McClelland, 1989) access to phonology is obligatory for reading in all orthographies, and there are more than just two possible routes for reading. In addition, the size of the units in the orthography-to-phonology mappings is determined by orthographic transparency, but also by reading proficiency and language characteristics, such as phonological and morphological structure (Frost, 2005; Perfetti, 2003; Perfetti et al., 2005; Ziegler and Goswami, 2005).

Beyond transparency and phonology

A comprehensive review by Share (2008b), suggests that an important aspect of reading, neglected by the theories formerly described is the familiarity of the word being read. The Lexical Quality Hypothesis (Perfetti, 2007) addressed this concern, and emphasizes the reader's experience. According to this hypothesis the quality and stability of lexical representations of written words determine the accuracy and fluency of word recognition and comprehension. Lexical quality is determined both by attributes of the reader (the individual's reading experience and their familiarity with the word) and by attributes of

* Corresponding author at: Psychology Department, University of Haifa, 199 Aba Khoushy Ave., Mt. Carmel, Haifa, Israel, 3498838.
E-mail addresses: ylweiss@gmail.com (W. Yael), katzirta@gmail.com (K. Tami), tbitan@research.haifa.ac.il (T. Bitan).

http://dx.doi.org/10.1016/j.neuroimage.2015.07.029
1053-8119/

the specific word (its phonology, orthography, frequency, etc.). Hence, in addition to the orthographic transparency of the writing system, word recognition is affected by multiple factors that vary across different orthographies, words and readers. Thus, for skilled readers, frequent word forms have good lexical quality that contributes to effective and stable retrieval of the word's identity (Perfetti, 2007).

Neural correlates of reading a transparent orthography

Inspired by the idea that orthographic transparency may affect the specific mechanisms involved in reading in different languages, a growing body of research addressed the effect of consistency between orthography and phonology by comparing between readers of transparent and opaque orthographies in different languages. For example, Paulesu et al. (2000) have found different brain activation in a PET study comparing oral word reading in English (opaque orthography) and Italian (transparent orthography) readers. English readers showed stronger activation in the left posterior inferior temporal gyrus and the anterior IFG suggested to be associated with a whole word lexical retrieval strategy, while Italians showed stronger activation in left superior temporal regions, associated with phonological processing. More recently a meta-analysis of reading studies in western and eastern orthographies showed that activation in the left temporo-parietal junction (TPJ; BA 39/40) was specific for alphabetic but not for non-alphabetic orthographies (Bolger et al., 2005). The effect of orthographic transparency was also found in the dorsal part of left IFG following training in an artificial script. This region showed greater activation for reading the alphabetic compared to the non-alphabetic script (Bitan et al., 2005).

Neuroimaging studies with bilinguals provide an opportunity to examine the effect of orthographic transparency within-subjects, but these effects often interact with language proficiency. For example, activation in the left inferior parietal lobule (IPL; BA 40) was related to reading Hindi which is more transparent than English when proficiency in both languages was balanced, and to reading in both orthographies when proficiency was greater in Hindi (Das et al., 2011). In contrast, in a study with Spanish-English bilinguals, activation in left IPL was related to reading English, although it was less transparent and more proficient than Spanish (Meschyan and Hernandez, 2006).

Orthographic familiarity effects on brain activation in word recognition are usually examined by comparing high to low frequency words, and between real and pseudowords. Neuroimaging studies in English, German and Japanese found that higher words' familiarity, frequency and imageability decreased activation in left IFG (Heim et al., 2012; Ischebeck et al., 2004; Pugh et al., 2008) and superior temporal gyrus (STG) for skilled readers (Pugh et al., 2008). These findings are consistent with reduced efforts in lexical and phonological access in familiar words.

Transparency and familiarity in the Hebrew orthography

Phonemes in Hebrew are represented with three graphemic systems: 18 letters that represent only consonants, four vowel letters (the אהוי (AHWY) letter set) that represent both vowels and consonants, and diacritic marks that represent vowels (Ravid, 2005). The inclusion of diacritic marks is optional, resulting in one script with two versions that differ in their orthographic transparency: an opaque writing system (unpointed—without diacritic marks) and a shallow writing system (pointed—with diacritic marks) (Bar-On, 2010; Share, 2008a). The unpointed opaque version includes mostly consonants graphemes, while vowel sounds are only partially represented by vowel letters. Moreover, some vowel letters are ambiguous because they represent more than one vowel, and a consonant. 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.

At the beginning stages of reading acquisition children learn to read the pointed script, which allows them to rely on serial bottom-up ortho-phono mapping to identify written words (Bar-On, 2010; Gur, 2005; Schiff et al., 2012; Shany et al., 2011). During the development of reading skills, diacritics become less crucial and are replaced by a greater reliance on higher-order word-level lexical and morphological information, while knowledge and use of diacritics declines over time (Bar-On, 2010).

While diacritics provide full and unambiguous vowel information, vowel letters provide only partial and ambiguous vowel information. All vowel letters denote both consonants and vowels, and some of them represent more than one vowel. For example, the letter 'ו' ('vav') can represent the consonant /v/ the vowel /o/, or the vowel /u/. Vowels at the end of words are almost always represented by vowel letters, while in the middle of a word /a/ and /e/ are never represented by a vowel letter, while /i/ and /o/ are represented by vowel letters in some words. However, in contrast to diacritics which are superimposed under or above the consonants, vowel letters are written in line with the consonants in a written word. Importantly, while the presence of diacritics is optional and may decrease familiarity with the words' orthographic pattern for adult readers, most Hebrew words appear consistently either with or without vowel letters, so vowel letters do not change the word familiarity. Thus, comparing the effects of diacritics and vowel letters enables us to examine different degrees of orthographic transparency, with stronger effects expected for diacritics as they provide more phonological information. However, we hypothesized that while vowel letters do not enhance orthographic transparency to the same degree as diacritics, they do not compromise familiarity either, hence their overall benefit for word recognition may be larger.

A large number of behavioral studies have examined the role of diacritics in word recognition for Hebrew readers at various stages of reading acquisition. Diacritics were found to facilitate word recognition in early stages of reading acquisition (Harel-koren, 2007; Navon and Shimron, 1981; Ravid, 1996; Shany et al., 2011; Shimron and Sivan, 1994). For skilled readers, different studies show mixed results: diacritics either facilitate (Koriat, 1984, 1985; Navon and Shimron, 1981; Shimron and Navon, 1982) or had no effect (Bentin and Frost, 1987; Harel-koren, 2007; Schiff and Ravid, 2004; Shimron and Sivan, 1994) on word recognition. Developmental studies suggest that in very early stages of reading acquisition Hebrew readers rely mostly on diacritics, and that the facilitating effect of vowel letters on word recognition develops over time with increasing exposure to unpointed words (Harel-koren, 2007; Schiff, 2003; Shany et al., 2011).

In our behavioral study (Weiss et al., 2015), skilled Hebrew readers showed an interaction of diacritics and word length in reading latency. In pointed words they demonstrated a classic length effect (longer words were read slower and less accurately than short words), while in unpointed words they demonstrated a reversed length effect (longer words were read faster and more accurately), suggesting reliance on mapping of smaller orthographic units in pointed compared to unpointed words. In contrast to the effect of diacritics, vowel letters, improved accuracy across all conditions, and decreased latency in unpointed words. The effect of vowel letters on reading latency specifically in unpointed words suggests that their facilitative effect is due to increased orthographic transparency.

Neural correlates of reading pointed words in Hebrew and Arabic

The research on the effect of diacritics on brain activity in Semitic languages is scarce. ERP studies that examined the role of diacritics in word recognition in Hebrew skilled readers have found that lexical decision of pointed as compared to unpointed words increased the amplitude and latencies of early negative components (N170), suggesting increased load on early visual-orthographic processing. In contrast, unpointed words increased the amplitude and decreased latencies of later components (~340 ms), suggesting greater reliance on lexical processing (Bar-Kochva, 2011; Bar-Kochva and Breznitz, 2012). To our knowledge, to date there is no fMRI study looking at the effect of diacritics in Hebrew. One fMRI study examined the effect of diacritic marks in adult Arabic readers, using a lexical decision task. In Arabic, as in Hebrew, diacritics that provide vowel information are omitted from text by 3rd grade, and adult Arabic readers are usually exposed to unpointed texts. Pointed Arabic words slowed lexical decision and increased activation in the insula and IFG, as compared to unpointed words, suggesting increased engagement of phonological and semantic processes. In contrast, unpointed words increased activation in the hippocampus and middle temporal gyri (MTG), suggesting increased lexical search (Bourisly et al., 2013).

Research predictions

In the current study we used fMRI to test the effect of orthographic transparency and familiarity on word recognition for skilled readers. We asked two questions: 1) *What is the effect of increasing orthographic transparency on the reader's brain? Does it facilitate or does it increase the load on orthographic phonological and lexical processes involved in word recognition? 2) How does orthographic transparency interact with the familiarity of the graphemic representation: does the effect of one overshadow the effect of the other?*

The effect of orthographic transparency was examined by comparing brain activation of reading pointed and unpointed words, and by comparing words with and without vowel letters. The effect of familiarity with the orthographic representations is evident in the comparison of pointed words (less familiar for adult Hebrew readers) and unpointed words (more familiar). To examine whether additional phonological information increases the reliance on assembled reading, we also manipulated the number of consonants, because word length effect is a sensitive indicator of assembled reading (De Luca et al., 2008; Ellis and Hooper, 2001; Ellis et al., 2004).

Based on the findings of our behavioral study (Weiss et al., 2015) that showed a facilitative effect of vowel letters, but not of diacritics, we predicted that familiarity will override the effect of orthographic transparency in the brain. Specifically we hypothesized that diacritics, which increase orthographic transparency while decreasing familiarity, would increase the load on word recognition, and thus increase brain activation. In contrast, vowel letters, which increase orthographic transparency without compromising familiarity, would decrease the load of word recognition, and thus decrease activation.

More specifically, our behavioral study (Weiss et al., 2015) suggested that diacritics enhance the reliance on assembled phonology (by showing a slowing effect of word length, specific to pointed words). We thus expect that pointed words would increase activation in brain areas associated with phonological representation (left STG), mapping of orthography to phonology (left IPL, left SMG), and phonological segmentation (left IFG pars opercularis). We also expect to find a similar interaction of word length and diacritics (more activation for longer words, only in the pointed condition) in these areas. Moreover, because pointed words are less familiar than unpointed words for adult Hebrew readers, they are also expected to increase activation in brain areas associated with visual and orthographic processing (occipital and ventral OT), and with lexical retrieval (IFG pars orbitalis and pars triangularis).

The facilitating effect of vowel letters in our behavioral study (Weiss et al., 2015), was evident not only in overall higher accuracy, but also in shorter latency specific to unpointed words, suggesting that vowel letters facilitate word recognition by facilitating the mapping of orthography to phonology. Many studies show reduced activation with increased proficiency (Dronjic and Bitan, In press). For example, when bilinguals were reading in their second less proficient language, increased activations were found in left IFG, MTG, STG and AG, as compared to reading in their first and more proficient language (Rüschemeyer et al., 2006; Buchweitz et al., 2009). In addition, neuroimaging studies found reduced activation for words with high familiarity, frequency and imageability in left IFG (Heim et al., 2012; Ischebeck et al., 2004, 2004; Pugh et al., 2008) and superior temporal gyrus (STG) (Pugh et al., 2008).We therefore predicted that the presence of vowel letters would decrease activation in these brain areas (left IFG, MTG, STG and AG).

Method

Participants

A group of 18 adults with average reading skills, 22:03–32:03 years old (M = 27:10, SD = 2.4, 7 males), was recruited from among graduate and undergraduate students in academic institutes. All participants were native Hebrew speakers, right-handed, and display normal (or corrected to normal) vision in both eyes. None of them had a history of learning disabilities, neurological or psychiatric disorders and were never diagnosed with reading impairments.

Because there are no standardized reading tests for adults in Hebrew, and based on previous studies (Ben-Yehudah and Ahissar, 2004; Katzir et al., 2004; Miller-Shaul, 2005), participant exclusion criteria was based on local norms collected in our lab from an independent sample of 191 unimpaired readers. Scores were obtained from the pseudoword and word reading accuracy within 1 min tests (Shatil, 1997a, 1997b), and participants were excluded if they scored less than one standard deviation below the average of the local norms in both tests. These norms are reported in Table 1.

Phonological decoding: *One Minute Pseudoword Test* (Shatil, 1997a)—In this test subjects read lists of pointed non-words as quickly and accurately as possible within 1 min. Number of correct words read within 1 min was counted.

Word reading: *One Minute Word Test* (Shatil, 1997b)—In this test subjects read lists of real unpointed words as quickly and accurately as possible within 1 min. Number of correct words read within 1 min was counted.

Participants' means and standard deviation of both measures are presented in Table 1

Stimuli

The stimuli consist of 192 Hebrew concrete nouns in four lists (48 words in each list) of two word lengths: 3 vs. 4 consonants; and two vowel letter conditions: with or without a vowel letter (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. As there is no available consensus corpus for written Hebrew frequency, our frequency ranking was based on subjective rating of ten elementary school teachers on a 1–5 Likert scale, that represent a range of average to high frequency in adult texts (see Table 2).

Experimental procedure

Each trial began with a 200 ms presentation of a fixation cross followed by the presentation of the stimulus word for 1500 ms and then a blank screen for 2300 ms. 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 MRI compatible microphone with noise cancellation (FOMRI™ III system, Optoacoustics Ltd.).

Table 1
Means and standard deviation of selection tests.

	Participants (N = 18)		Local norms (N = 191)		
	Mean number of correct words per minute	Standard deviation	Mean number of correct words per minute	Standard deviation	Criteria of 1 standard deviation below average
One Minute Word Tests	96.16	19.67	106.49	18.41	<88 correct words
One Minute Pseudoword Tests	61.22	7.77	61.04	14.146	<46.89 correct pseudowords

Stimuli were presented using E-Prime stimulus presentation software (v.2.0, Psychological Software Tools, Inc.). Pointed and unpointed 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 unpointed version. Four runs of pointed words and four runs of unpointed words appeared in alternating order, and the order was counter balanced across individuals. Stimuli from the current experiment were presented together with 56 words from another experiment (Weiss et al., in preparation) which were similar in length and frequency and appeared in both the pointed and unpointed 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'. 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/). A total of 592 trials were acquired in eight runs of 5:42 min. A practice list of ten different words was presented to participants immediately prior to the first experimental run.

fMRI data acquisition

Images were acquired using a 3.0 T 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 ms, 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, TR = 2000 ms. One hundred seventy-one images were acquired during each run. In addition, a high resolution, anatomical T1 weighted 3D structural images were acquired (AX SPGR, TR = 9.044 ms, TE = 3.0504 ms, 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.

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 0.8 mm (range = 0.1–3.5 mm). Sinc interpolation was used to minimize timing errors between slices (Henson et al., 1999). The functional images were coregistered with the anatomical image, and normalized to the standard T1 template volume (MNI). The data were then smoothed with a 5-mm isotropic Gaussian kernel.

Statistical analyses at the first level were done separately for pointed and unpointed words, in each participant using the GLM analysis for event-related designs. A high-pass filter with a cutoff period of 128 s 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 (3 vs. 4 consonants) as well as the baseline condition. The contrast of each basic condition vs. baseline, separately for pointed and unpointed words, was carried into the second level group analysis. Pointed and unpointed words were only compared at the second level. To avoid a possible effect of reduced brain response due to repetition of words across conditions (pointed and unpointed), 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.

Whole brain group analyses

Whole brain effects were assessed by means of the flexible factorial design with the factors subject, diacritics and vowel letters. Statistical mappings are depicted for descriptive purpose at significance level of $p < 0.05$ corrected for multiple comparisons, using a cluster extent threshold of $k \geq 50$.

ROI analyses

Regions of interest were anatomically defined based on brain areas known to be involved in visual word recognition in previous studies: left SMG and IPL associated with phonological decoding and mapping of orthography to phonology (Booth et al., 2007; Demonet et al., 1992; Fiebach et al., 2002; Graves et al., 2010; Jobard et al., 2003; Sandak et al., 2004; Xu et al., 2001); left AG associated with integration of orthography to semantics (Graves et al., 2010; Seghier, 2013); left MTG associated with semantic processing (Binder et al., 2009; Chou et al., 2006; Fiebach et al., 2002; Fiez, 1997; Jobard et al., 2003; Kircher et al., 2009; Paulesu et al., 1997); left FG associated with orthographic processing of written words in typical readers, and develops during reading experience (Booth et al., 2001; Dehaene et al., 2002; Jobard

Table 2
Examples of words for each experimental condition.

	4 consonants with vowel letter	4 consonants without vowel letter	3 consonants with vowel letter	3 consonants without vowel letter
With diacritics	גַּרְעִין	אַרְנָב	תִּירָס	דֶּלֶת
Without diacritics	גרעין	ארנב	תירס	דלת
	GRAIN	ARNV	TIRS	DLT
	/gara'in/	/a'rnav/	/tiras/	/delet/
	(nucleus)	(rabbit)	(corn)	(door)
Word frequency	3.221	3.409	3.399	3.269
mean and range	(1.333–4.75)	(1.25–4.875)	(1.417–4.917)	(1.125–5)

et al., 2003; Turkeltaub et al., 2003); left IFG pars opercularis associated with phonological segmentation (Burton et al., 2000; Hsieh et al., 2001; Poldrack et al., 2001); left IFG pars orbitalis and pars triangularis associated with lexical and semantic retrieval (Binder et al., 2009; Paulesu et al., 1997); and MOG associated with visual processing (Cohen et al., 2008). Five main cortical areas were identified in each hemisphere based on the literature. Within these main cortical areas 10 specific anatomical regions of interest were defined based on the Automated Anatomical Labeling atlas (AAL) (Tzourio-Mazoyer et al., 2002). The following ROIs were defined in the left hemisphere: 1) inferior frontal gyrus (IFG) including: pars opercularis (Oper), pars triangularis (Tri) and pars orbitalis (Orb); 2) temporo-parietal-junction (TPJ): including supramarginal gyrus (SMG), angular gyrus (AG) and inferior parietal lobule (IPL); 3) lateral temporal cortex (LTC): including middle temporal gyrus (MTG) and superior temporal gyrus (STG); 4) fusiform gyrus (FG); and 5) 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 et al., 2002). Differences in percent signal change (% signal change during a specific condition − % signal change during the asterisks baseline condition) were calculated for each participant in eight basic conditions (2 levels of diacritics × 2 levels of vowel letters × 2 levels of word length) in each ROI. Statistical analysis was done using IBM SPSS Statistics software (v. 19).

Separate GLM (General Linear Model) repeated measures analyses were conducted for each one of the five main cortical areas (IFG, TPJ, LTC, FG, MOG), with four within subject factors: ROI (for IFG, TPJ and LTC which included more than one ROI), diacritics, vowel letters and length and % signal change in each ROI as the dependent variable. No correction for multiple comparisons was applied, because all five cortical areas had specific predictions associated with them, and therefore these comparisons were planned. To test our predictions about the involvement of specific ROIs in different aspects of reading Hebrew, a follow-up analysis within each ROI was conducted for areas that showed a significant interaction of ROI with one or more experimental conditions. In addition, in each case of interaction between diacritics and one of the other experimental condition (vowel letters or length) further analyses were done separately for pointed and unpointed words.

Results

Whole brain analyses

The results of the whole brain group analysis are depicted for pointed and unpointed words compared to baseline in Fig. 1 and Table 3. Fig. 1 shows a larger extent of active voxels in pointed words in both left and right hemispheres. However, the comparison of pointed and unpointed words at the whole brain analysis did not survive the correction of multiple comparisons ($p < 0.05$ FWE corrected). This and other effects were further examined in planned comparisons at the ROI analysis.

ROI analyses

GLM analyses on % signal change were conducted for each main cortical area, with ROI, and all experimental conditions (diacritics, vowel letters and length) as within-subject factors. Significant main effects and interactions from these analyses, as well as follow-up analyses comparing between ROIs are summarized in Table 4.

A follow-up analysis within each ROI was conducted for areas that showed a significant interaction between ROI and one or more experimental conditions, namely left IFG, TPJ, and LTC. Significant main effects and interactions of these analyses, and of follow-up analyses for ROIs showing interaction of diacritics and one of the other experimental conditions, are presented in Table 5.

The following sections summarize the main effects found in the ROI analysis for each experimental factor: diacritics, vowel letters, word length, and the interactions of diacritics with vowel letters or with length.

Regions showing main effects of diacritics

Pointed words compared to unpointed words significantly increased activations in left IFG pars triangularis, but not in other parts of left IFG.

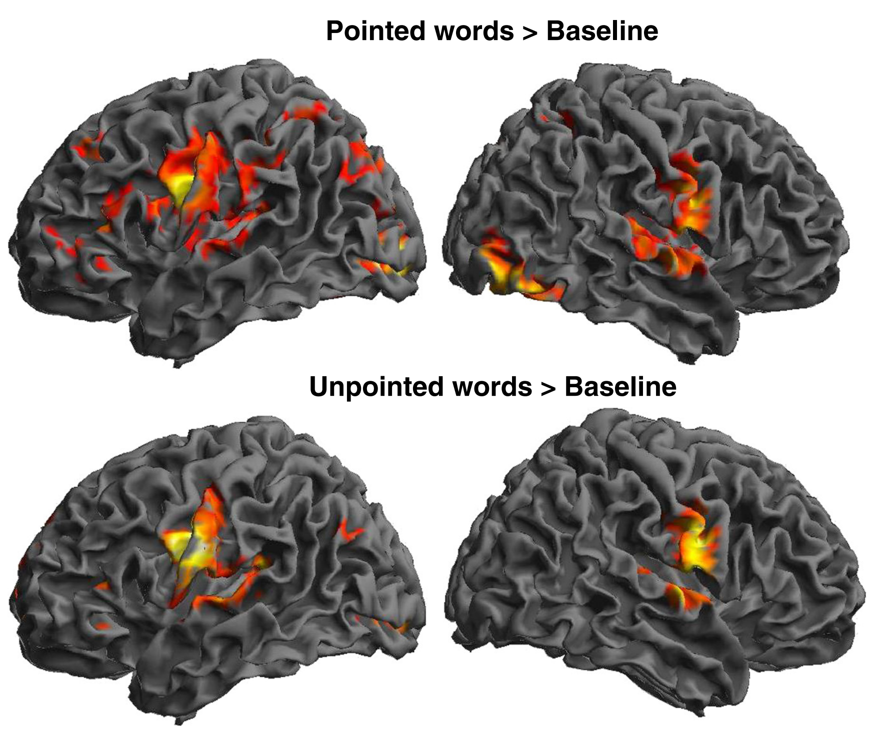

Fig. 1. Whole brain analysis. Activation for pointed and unpointed words compared to baseline (****). Threshold $p < 0.05$ FWE corrected with cluster extent $k \geq 50$.

Table 3
Activation in pointed and unpointed words vs. baseline. Threshold p < 0.05 FWE corrected with cluster extent k ≥ 50.

Area	BA	H	Z score	Voxels	X	Y	Z
Pointed words > Baseline							
Inferior/middle occipital gyrus	18/19	L	Inf	455	−36	−86	−2
Middle frontal gyrus–pars orbitalis	47	L	Inf	260	−28	38	−8
Precentral gyrus/postcentral gyrus/inferior parietal lobule	40/43	L	Inf	3698	−58	−2	20
Inferior/middle occipital gyrus	18/19	R	Inf	890	42	−84	−12
Middle occipital gyrus/cuneus/inferior parietal lobule/superior parietal lobule	7/39	L	Inf	609	−26	−74	24
Superior temporal gyrus/precentral gyrus	6/21	R	7.84	1985	62	−10	8
Inferior/middle frontal gyrus–pars orbitalis	47	R	7.32	100	32	38	−8
Precuneus/ posterior cingulated/calcarine	23	L	7.23	709	−2	−60	20
Cerebelum/culmen		R	7.23	184	18	−60	−26
Putamen/lentiform nucleus		L	7.19	924	−28	−12	−6
Superior/middle frontal gyrus	8	L	6.68	167	−18	26	42
Cerebelum/declive		L	6.66	72	−14	−62	−22
Inferior/middle frontal gyrus–pars triangularis	46	L	6.24	98	−48	42	0
Thalamus		R	5.84	86	20	−22	0
Superior parietal lobule	7	R	5.75	109	28	−56	58
Putamen/lentiform nucleus		R	5.48	72	28	−6	−8
Unpointed words > Baseline							
Postcentral gyrus/precentral gyrus	6	L	Inf	1951	−58	−14	24
Inferior/middle frontal gyrus–pars orbitalis	11	L	Inf	156	−28	36	−10
Inferior occipital gyrus/cuneus	18	L	Inf	140	−38	−80	−6
Precentral gyrus/rolandic operculum/superior temporal gyrus/transverse temporal gyrus	43	R	Inf	1297	56	−4	24
Cerebelum/declive		L	7.28	81	−14	−64	−20
Precuneus/calcarine/posterior cingulate	23	L	6.82	879	−2	−60	20
Amygdala/parahippocampal gyrus/putame/caudate		L	6.62	190	−20	−8	−16
Insula		L	6.60	71	−38	−14	16
Anterior cingulated/superior/middle frontal gyrus–pars orbitalis	32	L	6.46	898	−6	48	0
Cerebelum/declive		R	6.30	118	18	−64	−24
Inferior frontal gyrus–pars triangularis	45	L	6.22	55	−46	28	10
Anterior cingulate	32	L	5.89	148	−4	22	32
Thalamus		L	5.85	126	−8	−12	14
Angular gyrus	39	L	5.54	66	−46	−72	32

Pointed words have also significantly increased activation in left SMG and IPL, but not in left AG, with a larger effect of diacritics in left IPL compared to the other TPJ regions. Finally, pointed words showed greater activation in left MOG (see Fig. 2). No region showed greater activation in unpointed compared to pointed words.

Regions showing main effect of vowel letters and its interaction with diacritics

Words with vowel letters compared to words without vowel letters significantly decreased activations in left IFG pars opercularis, SMG and IPL (see Fig. 3a). In addition, decreased activation for words with vowel

Table 4
Significant main effects and interactions in main cortical areas. *p ≤ .05, **p ≤ .01, ***p ≤ .001.

Area	Effect	df	F
L.IFG	With vowel letter < Without vowel letter	17	34.867***
	ROI × Vowel letter	16	8.689**
	Vowel letter effect–L.Oper > L.Tri	1	7.965**
	Diacritics × Vowel letter	17	5.919*
	Diacritics × Length × Vowels	17	4.935*
L.TPJ	Pointed > Unpointed	17	8.840**
	With vowel letter < Without vowel letter	17	12.650**
	ROI × Diacritics	16	8.065**
	Diacritics effect–L.IPL > L.SMG	1	12.44**
	Diacritics effect–L.IPL > L.AG	1	9.598**
	ROI × vowel letter	16	4.699*
	Vowel letter effect–L.IPL > L.AG	1	4.566*
	ROI × Diacritics × Vowel letter	16	3.737*
	ROI × Length × Vowel letter	16	5.210*
L.LTC	STG > MTG	17	68.322***
	Long words > Short words	17	5.010*
	ROI × Length	17	22.265***
	Diacritics × Length × Vowel letter	17	4.463*
L.FG			N.S.
L.MOG	Pointed > Unpointed	17	14.899***
	Long words > Short words	17	13.122**
	Diacritics × Length	17	12.087**
	Length effect only in pointed words	17	20.544***

Table 5
Significant main effects and interactions within ROIs. *p ≤ .05, **p ≤ .01, ***p ≤ .001.

ROI	Effect	df	F
L.IFG			
Orb	With vowel letter < Without vowel letter	17	13.778**
	Diacritics × Vowel letter	17	6.138*
	Vowel letter effect only in unpointed words	17	14.133**
Tri	With diacritics > Without diacritics	17	6.612**
	With vowel letter < Without vowel letter	17	12.911**
	Diacritics × Vowel letter	17	5.369*
	Vowel letter effect only in unpointed words	17	11.047**
Oper	With vowel letter < Without vowel letter	17	37.645***
L.TPJ			
SMG	Pointed > Unpointed	17	4.752*
	With vowel letter < Without vowel letter	17	13.525**
AG	Diacritics × Vowel letter	17	6.904*
	Vowel letter effect only in unpointed words	17	8.042*
IPL	Pointed > Unpointed	17	15.530***
	With vowel letter < Without vowel letter	17	16.338***
	Diacritics × Length	17	6.749*
	Length effect only in pointed words	17	5.803*
L.LTC			
MTG	With vowel letter < Without vowel letter	17	4.958*
	Diacritics × Vowels	17	8.282**
	Vowel letter effect only in unpointed words	17	10.593**
STG	Long words > Short words	17	8.925**

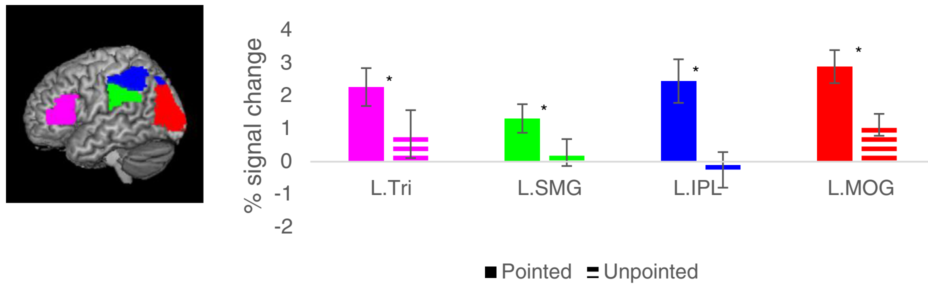

Fig. 2. Main effect of diacritics. ROIs showing a main effect of diacritics: L.Tri (left IFG pars triangularis), L.SMG (left supramarginal gyrus), L.IPL (left inferior parietal lobule) and L.MOG (left middle occipital gyrus). Significant effects ($p < .05$) are marked by asterisks.

letters, only in unpointed words, was found in left MTG, IFG pars triangularis, IFG pars orbitalis, and AG (see Fig. 3b).

Regions showing effects of word length and its interaction with diacritics

Longer words (with four consonants) showed more activation than shorter words (with three consonants) in left STG (see Fig. 4). In addition, increased activation for long compared to short words was specific to the pointed condition in left IPL, and MOG (see Fig. 4).

Discussion

This study is the first fMRI study to examine the effect of orthographic transparency in reading Hebrew words. Nevertheless, reading pointed words engages with more extensive activation in both left and right hemispheres as compared to unpointed words.

The current study examined the effects of orthographic transparency and familiarity in a within-subject within-language design. Increasing orthographic transparency by adding vowel information resulted in drastically different activation patterns depending on the familiarity of the graphemic representations, evident in regions involved in phonological, orthographic and semantic processing.

The neural networks of reading pointed vs. unpointed words

Our finding of greater activation in left SMG and left IPL for pointed (less familiar and more transparent) compared to unpointed words are consistent with our predictions and with previous studies. These regions have been previously implicated in mapping of orthography to phonology (Bitan et al., 2007; Das et al., 2011; Graves et al., 2010; Jobard et al., 2003) suggesting that reading of pointed words increases the load on these processes. It should also be noted that no effect of diacritics was found in the adjacent AG, consistent with the hypothesis that this region is associated with mapping of orthography to semantic representations (Graves et al., 2010; Seghier, 2013) which is not expected to be affected by diacritics.

Interestingly, studies show increased activation in left IPL for: alphabetic as compared to non-alphabetic orthographies (Bolger et al., 2005); phonetic (pinyin) as compared to logographic orthographies (Chinese) (Chen et al., 2002); and transparent alphabetic (Hindi) as compared to less transparent alphabetic orthographies (English) (Das et al., 2011). Although these results may suggest greater reliance on mapping of orthography to phonology in more transparent orthographies, as always with fMRI results, greater activation may indicate either greater reliance on a cognitive process or greater difficulty with that process. Accordingly, greater activation in left IPL was also found in bilinguals for the less

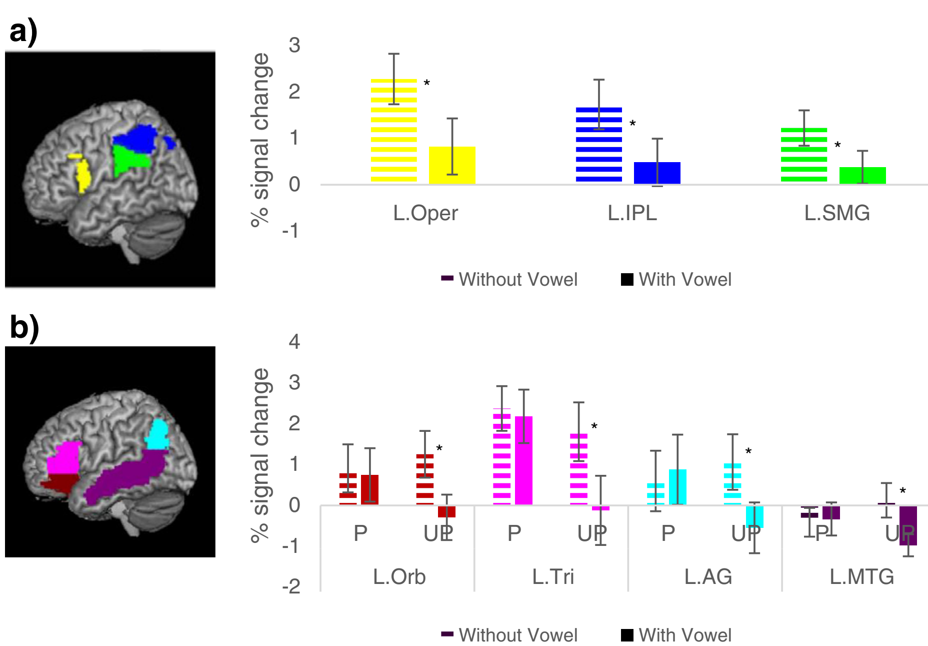

Fig. 3. Effect of vowel letters. ROIs showing a main effect of vowel letter: (a) L.Oper (left IFG pars opercularis), L.SMG (left supramarginal gyrus), L.IPL (left inferior parietal lobule) and (left middle occipital gyrus). ROIs showing an effect of vowel letter only in unpointed words (UP) and (b) L.MTG (left middle temporal gyrus), L.Tri (left IFG pars triangularis), L.Orb (left IFG pars orbitalis) and L.AG (left angular gyrus). Significant effects ($p < .05$) are marked by asterisks.

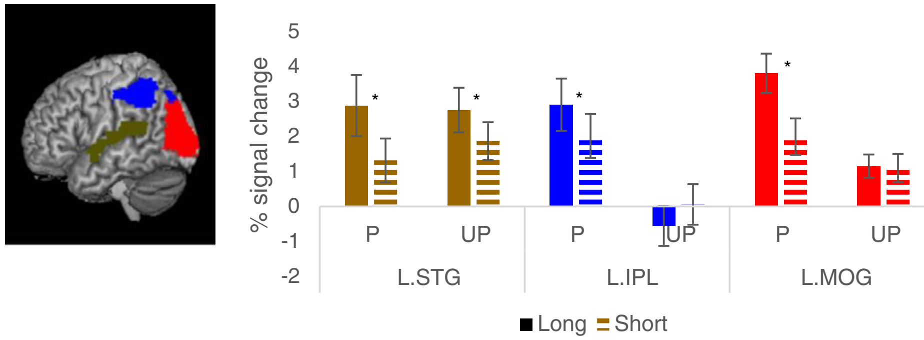

Fig. 4. Effect of word length. ROIs that show main effect of word length: L.STG (left superior temporal gyrus) and ROIs that show word length effect only in pointed words (P): L.IPL (left inferior parietal lobule) and L.MOG (left middle occipital gyrus). Significant effects ($p < .05$) are marked by asterisks.

transparent orthography (English as compared to Spanish) (Meschyan and Hernandez, 2006). Moreover, when reading English words the left IPL showed increased activation for words with an inconsistent mapping of orthography to phonology (Bitan et al., 2007), suggesting that the opaque mapping of orthography to phonology may increase the load on the mapping process. This interpretation is also consistent with the finding that left IPL was associated with effortful phonological retrieval of an unfamiliar orthographic form (Romanized Hindi) (Rao et al., 2013). These results suggest that the recruitment of left IPL in pointed words in the current study may not only reflect the greater reliance on mapping orthography to phonology due to the orthographic transparency or pointed words, but also the fact that their graphemic representation is less familiar, and thus mapping it to phonology is more effortful.

Our results further show a significant interaction of diacritics and word length, with more activation in long than in short words only for pointed words, in left IPL and MOG. This interaction is consistent with our prediction and with our behavioral findings (Weiss et al., 2015) showing a slowing effect of word length only for pointed words. Thus, only for the less familiar pointed words, an additional consonant increased processing load in both visual processing areas (MOG) and areas related to mapping of orthography to phonology (left IPL). These results are consistent with previous studies showing in occipital and parietal regions a specific effect of word length for pseudo words in German (Schurz et al., 2010) and for visually degraded words in French (Cohen et al., 2008). These results suggest that in the current study, the presence of diacritic marks reduced the familiarity of the visual word forms, resulting in a piecemeal processing of smaller orthographic units.

In addition to the predicted effects of diacritics, we found that pointed as compared to unpointed words increased activation in left inferior frontal gyrus (IFG) pars triangularis, associated with semantic working memory and lexical retrieval (Fiebach et al., 2002; Gabrieli et al., 1998; Jobard et al., 2003; Kircher et al., 2009; Paulesu et al., 1997). This finding is consistent with the conclusion that the presentation of diacritics reduced the familiarity of the word form, resulting in increased load on the process of lexical retrieval.

The neural effect of vowel letters

As predicted, in contrast to the increased activation found for pointed word, vowel letters, which increase orthographic transparency without compromising familiarity, decreased activation in the left SMG and IPL as well as in left IFG pars opercularis. These results can be interpreted in one of two ways: first, the presence of vowel letters may facilitate the mapping of orthographic to phonological representations (left SMG and IPL), and the phonological segmentation processes (left IFG opercularis), as they provide more phonological information. Alternatively, the presence of vowel letter may decrease the engagement of ortho-phono mapping in word recognition, while increasing the reliance on lexical and semantic mechanisms. However, no region (associated with lexical/semantic processing or another) showed increased activation in the presence of vowel letters, rendering this interpretation less plausible.

Interestingly, our results also show decreased activation for words with vowel letters specific to unpointed words, in left AG, MTG, IFG pars triangularis and IFG pars orbitalis. These regions have been associated with lexical retrieval (IFG pars triangularis, and pars orbitalis), semantic processing (MTG), and mapping of orthography to semantics (AG) (Binder et al., 2009; Fiebach et al., 2002; Fiez, 1997; Graves et al., 2010; Jobard et al., 2003; Kircher et al., 2009; Paulesu et al., 1997). 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 unpointed words (Weiss et al., 2015). These results suggest that while vowel letter facilitate the mapping or orthography to phonology regardless of diacritics (as suggested by the main effect of vowel letters in left SMG and IPL), only in the absence of diacritic marks the presence of vowel letters facilitate the lexical and semantic access.

The effect of an additional vowel letter on brain activation was dramatically different from that of an additional consonant, as evident in the main effect of word length. While vowel letter reduced the activation in brain areas related to mapping of orthography to phonology (left SMG and IPL) and phonological segmentation (left IFG opercularis), an additional consonant increased activation in left STG related to phonological processing. Our behavioral study suggested that the addition of any letter (a consonant or a vowel) reduces the competition from orthographic neighbors, and may thus explain the facilitation of these manipulations especially in unpointed words (Weiss et al., 2015). The differences in brain activation suggest that the effect of vowel letters is different from that of an additional consonant letter, and results from their contribution to orthographic transparency. However, the effect of vowel letters was also different from the effect of diacritics, despite the fact that both of them increase orthographic transparency. Thus, vowel letters have a unique role in word recognition in Hebrew and may facilitate access to the word's meaning, as they increase orthographic transparency while still being very familiar to the adult Hebrew reader.

Conclusions

Findings from the current study indicate that both orthographic transparency and familiarity play a role in word recognition. In terms of the Lexical Quality Hypothesis (Perfetti, 2007), these results suggest that when increasing the orthographic transparency using a familiar graphemic representation, it improves lexical quality and thus improves word recognition. A familiar representation that increases orthographic transparency, as vowel letters do in Hebrew script, decreases the demands on word recognition as reflected in relief on ortho-phono-mapping, phonological and semantic processing. On the other hand, when the graphemic representation is less familiar it decreases lexical quality, even though it increases orthographic transparency, and thus it results in greater demands on word recognition. Altogether these results suggest that familiarity overrides the effect of orthographic transparency. Finally, in line with the connectionists point of view (Seidenberg and McClelland, 1989), both transparency and familiarity effects are not restricted to specific processing mechanism (such as phonological or visual processing), but exist in all mechanisms involved in word recognition in different weights.

Acknowledgments

This work was supported by the ISF 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 standard deviation 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

Bar-Kochva, I., 2011. Does processing a shallow and a deep orthography produce different brain activity patterns? An ERP study conducted in Hebrew. Dev. Neuropsychol. 36 (7), 933–938.

Bar-Kochva, I., Breznitz, Z., 2012. Does the reading of different orthographies produce distinct brain activity patterns? An ERP study. PLoS One 7 (5) (e36030).

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

Bentin, S., Frost, R., 1987. Processing lexical ambiguity and visual word recognition in a deep orthography. Mem. Cogn. 15 (1), 13–23. http://dx.doi.org/10.3758/BF03197708.

Ben-Yehudah, G., Ahissar, M., 2004. Sequential spatial frequency discrimination is consistently impaired among adult dyslexics. Vis. Res. 44 (10), 1047–1063. http://dx.doi.org/10.1016/j.visres.2003.12.001.

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. Cereb. Cortex (New York, N.Y.: 1991) 19 (12), 2767–2796. http://dx.doi.org/10.1093/cercor/bhp055.

Bitan, T., Manor, D., Morocz, I.A., Karni, A., 2005. Effects of alphabeticality, practice and type of instruction on reading an artificial script: an fMRI study. Cogn. Brain Res. 25 (1), 90–106.

Bitan, T., Burman, D.D., Chou, T., Lu, D., Cone, N.E., Cao, F., . . ., Booth, J.R., 2007. The interaction between orthographic and phonological information in children: an fMRI study. Hum. Brain Mapp. 28 (9), 880–891.

Bolger, D.J., Perfetti, C.A., Schneider, W., 2005. Cross-cultural effect on the brain revisited: universal structures plus writing system variation. Hum. Brain Mapp. 25 (1), 92–104. http://dx.doi.org/10.1002/hbm.20124.

Booth, J.R., Burman, D.D., Santen, F.W.V., Harasaki, Y., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2001. The development of specialized brain systems in reading and oral-language. Child Neuropsychol. 7 (3), 119–141.

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://dx.doi.org/10.1016/j.neuropsychologia.2006.08.015.

Bourisly, A.K., Haynes, C., Bourisly, N., Mody, M., 2013. Neural correlates of diacritics in Arabic: an fMRI study. J. Neurolinguistics 26 (1), 195–206.

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.

Buchweitz, A., Mason, R.A., Hasegawa, M., Just, M.A., 2009. Japanese and English sentence reading comprehension and writing systems: An fMRI study of first and second language effects on brain activation. Bilingualism: Language and Cognition 12 (02), 141–151.

Burton, M., Small, S., Blumstein, S., 2000. The role of segmentation in phonological processing: an fMRI investigation. Cogn. Neurosci., J. 12 (4), 679–690.

Chen, Y., Fu, S., Iversen, S.D., Smith, S.M., Matthews, P.M., 2002. Testing for dual brain processing routes in reading: a direct contrast of Chinese character and pinyin reading using fMRI. J. Cogn. Neurosci. 14 (7), 1088–1098. http://dx.doi.org/10.1162/089892902320474535.

Chou, T., Booth, J.R., Bitan, T., Burman, D.D., Bigio, J.D., Cone, N.E., . . ., Cao, F., 2006. Developmental and skill effects on the neural correlates of semantic processing to visually presented words. Hum. Brain Mapp. 27 (11), 915–924.

Cohen, L., Dehaene, S., Vinckier, F., Jobert, A., Montavont, A., 2008. Reading normal and degraded words: contribution of the dorsal and ventral visual pathways. NeuroImage 40 (1), 353–366. http://dx.doi.org/10.1016/j.neuroimage.2007.11.036.

Coltheart, M., Rastle, K., Perry, C., Langdon, R., Ziegler, J., 2001. DRC: a dual route cascaded model of visual word recognition and reading aloud. Psychol. Rev. 108 (1), 204.

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

Das, T., Padakannaya, P., Pugh, K., Singh, N., 2011. Neuroimaging reveals dual routes to reading in simultaneous proficient readers of two orthographies. NeuroImage 54 (2), 1476–1487.

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. Cogn. Behav. Neurol.: Official Journal of the Society for Behavioral and Cognitive Neurology 21 (4), 227.

Dehaene, S., Le Clec'H, G., Poline, J.B., Le Bihan, D., Cohen, L., 2002. The visual word form area: a prelexical representation of visual words in the fusiform gyrus. Neuroreport 13 (3), 321–325.

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

Dronjic, V., Bitan, T., 2015. Reading Brain and Cognition. In: Chen, X., Dronjic, V., Helms-Park, R. (Eds.), Reading in a Second Language: Cognitive and Psycholinguistic Issues. Routledge (in press).

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. Appl. Psycholinguist. 22 (4), 571–599.

Ellis, N.C., Natsume, M., Stavropoulou, K., Hoxhallari, L., Daal, V.H.P., Polyzoe, N., . . ., Petalas, M., 2004. The effects of orthographic depth on learning to read alphabetic, syllabic, and logographic scripts. Read. Res. Q. 39 (4), 438–468.

Fiebach, C., Friederici, A., Müller, K., Cramon, D.v., 2002. fMRI evidence for dual routes to the mental lexicon in visual word recognition. Cogn. Neurosci., J. 14 (1), 11–23.

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

Frost, R., 2005. Orthographic systems and skilled word recognition processes in reading. *The Science of Reading: A Handbook* pp. 272–295.

Frost, R., 2012. Towards a universal model of reading. Target article. Behav. Brain Sci. 35 (5), 263–279.

Gabrieli, J.D., Poldrack, R.A., Desmond, J.E., 1998. The role of left prefrontal cortex in language and memory. Proc. Natl. Acad. Sci. U. S. A. 95 (3), 906–913.

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.

Gur, T. (2005). *Reading Hebrew vowel diacritics: A longitudinal investigation from grade 1 to grade 3.* (Unpublished PhD). University of Haifa, Haifa. Israel.

Harel-koren, D., 2007. *The effectiveness of orthographic representations of vowels signs in Hebrew: developmental aspect* (Master).

Heim, S., Wehnelt, A., Grande, M., Huber, W., Amunts, K., 2012. Effects of lexicality and word frequency on brain activation in dyslexic readers. Brain Lang. http://dx.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–?.

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

Ischebeck, A., Indefrey, P., Usui, N., Nose, I., Hellwig, F., Taira, M., 2004. Reading in a regular orthography: an fMRI study investigating the role of visual familiarity. J. Cogn. Neurosci. 16 (5), 727–741.

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.

Katz, L., Frost, R., 1992. The Reading Process Is Different for Different Orthographies: The Orthographic Depth Hypothesis.

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. Read. Writ. 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. Hum. Brain Mapp. 30 (12), 4116–4128.

Koriat, A., 1984. Reading without vowels: lexical access in Hebrew. In: Bouma, H., Bouwhuis, D.G. (Eds.), Attention and performance. NJ: Lawrence Erlbaum, Hillsdale, pp. 1–15.

Koriat, A., 1985. Lexical access for low-and high-frequency words in Hebrew. Mem. Cogn. 13 (1), 37–44.

McClelland, J.L., Rumelhart, D.E., 1981. An interactive activation model of context effects in letter perception: I. an account of basic findings. Psychol. Rev. 88 (5), 375–407. http://dx.doi.org/10.1037/0033-295X.88.5.375.

Meschyan, G., Hernandez, A.E., 2006. Impact of language proficiency and orthographic transparency on bilingual word reading: an fMRI investigation. NeuroImage 29 (4), 1135–1140.

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.

Navon, D., Shimron, J., 1981. Does word naming involve grapheme-to-phoneme translation? Evidence from Hebrew. J. Verbal Learn. Verbal Behav. 20 (1), 97–109.

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

Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S.F., . . ., Lorusso, M., 2000. A cultural effect on brain function. Nat. Neurosci. 3, 91–96.

Perfetti, C.A., 2003. The universal grammar of reading. Sci. Stud. Read. 7 (3), 24.

Perfetti, C.A., 2007. Reading ability: lexical quality to comprehension. Sci. Stud. Read. 11 (4), 1–27.

Perfetti, C.A., Liu, Y., Tan, L.H., 2005. The lexical constituency model: some implications of research on Chinese for general theories of reading. Psychol. Rev.; Psychol. Rev. 112 (1), 43.

Poldrack, R.A., Temple, E., Protopapas, A., Nagarajan, S., Tallal, P., Merzenich, M., Gabrieli, J.D., 2001. Relations between the neural bases of dynamic auditory processing and phonological processing: evidence from fMRI. J. Cogn. Neurosci. 13 (5), 687–697.

Pugh, K., Frost, S.J., Sandak, R., Landi, N., Rueckl, J.G., Constable, R.T., . . ., Mencl, W.E., 2008. Effects of stimulus difficulty and repetition on printed word identification: an fMRI comparison of nonimpaired and reading-disabled adolescent cohorts. J. Cogn. Neurosci. 20 (7), 1146–1160.

Rao, C., Mathur, A., Singh, N.C., 2013. 'Cost in transliteration': the neurocognitive processing of romanized writing. Brain Lang. 124 (3), 205–212.

Ravid, D., 1996. Accessing the mental lexicon: evidence from incompatibility between representation of spoken and written morphology. Linguistics 34 (6), 1219–1246.

Ravid, D., 2005. Hebrew orthography and literacy. In: Joshi, R., Aaron, P.G. (Eds.), *Handbook of Orthography and Literacy*. NJ: Erlbaum, Mahwah, pp. 339–364.

Rüschemeyer, S.A., Zysset, S., Friederici, A.D., 2006. Native and non-native reading of sentences: an fMRI experiment. Neuroimage 31 (1), 354–365.

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. Sci. Stud. Read. 8 (3), 273–292.

Schiff, R., 2003. The effects of morphology and word length on the reading of Hebrew nominals. Read. Writ. 16 (4), 263–287. http://dx.doi.org/10.1023/A:1023666419302.

Schiff, R., Ravid, D., 2004. Representing written vowels in university students with dyslexia compared with normal Hebrew readers. Ann. Dyslexia 34 (1), 39–64. http://dx.doi.org/10.1007/s11881-004-0003-2.

Schiff, R., Katzir, T., Shoshan, N., 2012. Reading accuracy and speed of vowelized and unvowelized scripts among dyslexic readers of Hebrew: the road not taken. Ann. Dyslexia http://dx.doi.org/10.1007/s11881-012-0078-0.

Schurz, M., Sturm, D., Richlan, F., Kronbichler, M., Ladurner, G., Wimmer, H., 2010. A dual-route perspective on brain activation in response to visual words: evidence for a length by lexicality interaction in the visual word form area (VWFA). NeuroImage 49 (3), 2649–2661.

Seghier, M.L., 2013. The angular gyrus: multiple functions and multiple subdivisions. The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry 19 (1), 43–61. http://dx.doi.org/10.1177/1073858412440596.

Seidenberg, M.S., McClelland, J.L., 1989. A distributed, developmental model of word recognition and naming. Psychol. Rev. 96 (4), 523.

Shany, M., Bar-On, A., Katzir, T., 2011. Reading different orthographic structures in the shallow-pointed Hebrew script: a cross-grade study in elementary school. Read. Writ. 1–22.

Share, D.L., 2008a. On the anglocentricities of current reading research and practice: the perils of overreliance on an "outlier" orthography. Psychol. Bull. 134 (4), 584.

Share, D.L., 2008b. Orthographic learning, phonological recoding, and self-teaching. Adv. Child Dev. Behav. 36, 31–82.

Shatil, E., 1997a. *One-minute test for pseudowords - unpublished test*. University of Haifa, Haifa.

Shatil, E., 1997b. *One-minute test for words- unpublished test*. University of Haifa, Haifa.

Shimron, J., Navon, D., 1982. The dependence on graphemes and on their translation to phonemes in reading: a developmental perspective. Read. Res. Q. 210–228.

Shimron, J., Sivan, T., 1994. Reading proficiency and orthography evidence from Hebrew and English. Lang. Learn. 44 (1), 5–27.

Turkeltaub, P.E., Gareau, L., Flowers, D.L., Zeffiro, T.A., Eden, G.F., 2003. Development of neural mechanisms for reading. Nat. Neurosci. 6 (7), 767–773.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., . . ., Joliot, M., 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.

Weiss, Y., Katzir, T., Bitan, T., 2015. Effects of orthographic transparency and morphological complexity on brain of typical and dyslexic adults Hebrew readers in preparation.

Weiss, Y., Katzir, T., Bitan, T., 2015. Effect of orthographic transparency and familiarity on reading Hebrew words in dyslexic and typical readers. Ann. Dyslexia 65 (2).

Xu, B., Grafman, J., Gaillard, W.D., Ishii, K., Vega-Bermudez, F., Pietrini, P., . . ., Theodore, W., 2001. Conjoint and extended neural networks for the computation of speech codes: the neural basis of selective impairment in reading words and pseudowords. Cereb. 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. Psychol. Bull. 131 (1), 3.