Hebrew Brain vs. English Brain: Language Modulates the Way It Is Processed

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Abstract

■ Is language processing universal? How do the specific properties of each language influence the way it is processed? In this study, we compare the neural correlates of morphological processing in Hebrew—a Semitic language with a rich and systematic morphology, to those revealed in English—an Indo-European language with a linear morphology. Using fMRI, we show that while in the bilingual brain both languages involve a common neural circuitry in processing morphological structure, this activation is significantly modulated by the different aspects of language. Whereas in Hebrew, morphological processing is independent of semantics, in English, morphological activation is clearly modulated by semantic overlap. These findings suggest that the processes involved in reading words are not universal, and therefore impose important constraints on current models of visual word recognition. ■

INTRODUCTION

Is language processing universal? Are there qualitative differences in processing different languages? If so, how do the specific properties of the language modulate the way it is processed? These theoretical questions have been the focus of heated debates in neurocognitive research. A large corpus of behavioral studies that have focused on cross-linguistic comparisons has, so far, not produced unequivocal results. In the present study, we attempt to address these issues by considering imaging data of morphological processing during reading.

As a general approximation, current computational models of reading are implicitly universal, and they do not consider themselves to be language specific. Hence, current opinion posits that although languages differ in the statistical distribution of letters or letter clusters, printed words in English, Spanish, or French are assumed to be processed and recognized alike. However, the question whether similar principles of lexical processing are shared by two languages becomes intriguing when the two languages come from different language families, such that they do not share linguistic representations.

In this context, comparing morphological processing of printed words in Semitic and Indo-European languages has been drawing significant attention. Morphology concerns the internal structure of words. It enables languages to convey similar meanings by preserving a part of the word's form (e.g., heal–health). Hence, it is reflected by systematic correlations of form (orthography, phonology) and meaning (semantics). Languages, however, differ in their morphological properties and in how they create morphological complexity. In this study, we focus on Hebrew and English, which represent two different types of linguistic systems. Hebrew, like other Semitic languages, has a rich and systematic morphology where most words are morphologically complex and consist of derivations of triconsonantal root morphemes (see Frost, Forster, & Deutsch, 1997 for a detailed description of Hebrew morphology). Hebrew words are thus formed by intertwining consonant root morphemes and phonological word-pattern morphemes. English morphology, on the other hand, is characterized by a linear and sequential concatenation of prefixes or suffixes to a base morpheme, which forms multimorphemic words. In contrast to Hebrew, the base morphemes in most cases constitute word forms in their own right (such as *dark* in *darkness*, or *dream* in *dreamer*), and their orthographic and phonological integrity remains intact.

Behavioral studies investigating the relation between morphological processing and semantic and orthographic processing consistently suggest that reading processes in Hebrew and in English differ qualitatively. The main difference seems to be that in English (as in other Indo-European languages), the processing system is tuned to the word's linear orthographic structure, whereas in Hebrew, the processing system automatically searches for the root letters. This is because words in the Hebrew mental lexicon have been shown to be organized by morphology, that is, by root families rather than by simple letter sequences (Frost, 2009; Frost et al., 1997). Regarding morphological processing, a significant difference between Hebrew and English concerns the interplay of

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semantic similarity and the perception of morphological relatedness. Several studies have shown that the extent of semantic overlap between two Hebrew words that share the same root (and thus, are morphologically related) does not seem to have any effect on the perception of morphological relatedness (Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003; Frost, Deutsch, Gilboa, Tannenbaum, & Marslen-Wilson, 2000; Frost et al., 1997). In contrast, for English readers, the results seem to be much less consistent and do not present an unequivocal pattern. Some masked priming studies show that semantically transparent (e.g., farmer–farm), semantically opaque (e.g., department–depart), or pseudoderivations (e.g., irony–iron) are treated alike, suggesting that, similar to Hebrew, a semantic overlap between derivations does not play any role in word recognition (see Rastle & Davis, 2008 for a review). However, other studies demonstrate that morphological processing is clearly modulated by semantic considerations (Diependaele, Sandra, & Grainger, 2005; Giraudo & Grainger, 2001; Feldman, 2000). These results in English, however, intermix different research paradigms and therefore may tap different processing stages of morphological information.

The difference between Hebrew and English is reflected in imaging studies as well: fMRI results in Hebrew consistently reveal a network involved in morphological processing that is not influenced by the semantic properties of the stimuli. This was found for both explicit (Bick, Goelman, & Frost, 2008) and implicit processing (Bick, Frost, & Goelman, 2010). In contrast, fMRI results in English, again, do not present a clear and unequivocal picture. Devlin, Jamison, Matthews, and Gonnerman (2004) found no evidence of morphological processing that could not be explained by semantics or orthography. However, both Bozic, Marslen-Wilson, Stamatakis, Davis, and Tyler (2007) and Gold and Rastle (2007) did find regions showing independent morphological processing, but the locations of these regions were inconsistent. Several event-related potential (ERP) studies have investigated the relation between morphological processing and semantics, but have again reported contradicting results: Although some found no effect of semantic transparency (Koester & Schiller, 2008; Lavric, Clapp, & Rastle, 2007), others could not clearly report an effect of morphological relatedness for semantically opaque words (Morris, Frank, Grainger, & Holcomb, 2007). These contradicting results challenge the view that considers orthographic, phonological, and semantic sublinguistic units to be the main building blocks of language (Seidenberg & McClelland, 1989), and questions whether morphology should be regarded as a distinct level of lexical architecture or a simple interplay of form and meaning.

The present study was designed to investigate whether the morphological structure of the language influences the way it is processed in the brain. More specifically, we were concerned with the following question: Do Hebrew–English bilinguals use a common neural network when processing morphology in the two languages? If so, does the network display similar neural patterns of activation when processing morphological information for Hebrew and for English material?

Extensive research has addressed the question of the multiple representations of words in the bilingual lexical system. Hence, models such as the Revised Hierarchical Model (RHM; Kroll & Stewart, 1994), or the Bilingual Interactive Activation model (BIA; Dijkstra & Van Heuven, 1998), provided a description of how exactly one's native language (L1) and languages learned later in life (L2) conceptual and lexical links constantly interact in the bilingual brain, and how automaticity and inhibitory control develop in proficient bilinguals. In general, most of these studies focused on relatively skilled adult bilinguals, showing that successful L2 learning consists of developing new linguistic representations, and that this process requires cognitive support of executive functions (see Kroll & Tokowicz, 2005, for an extensive review). Imaging studies have demonstrated the relation between the neural representation of subject's L1 and L2 (e.g., Chee, 2006; Chee, Soon, Lee, & Pallier, 2004; Mahendra, Plante, Magloire, Milman, & Trouard, 2003; Tan et al., 2003) defining the neural correlates involved in the control of language switching (Hernandez, 2009; Abutalebi et al., 2008; Rodriguez-Fornells, Rotte, Heinze, Nosselt, & Munte, 2002). Beyond understanding bilingualism itself, presenting bilinguals with linguistic stimuli in the two languages is used to allow a well balanced comparison between the processing of the two languages. Such was conducted recently by Lehtonen et al. (2009), who compared processing of inflectional morphology in Finnish–Swedish bilinguals. They found a fronto-temporal increase in activation when nouns were morphologically complex relative to monomorphemic only in Finnish but not in Swedish. As subject and environment conditions were identical in both languages, the plausible interpretation would be that these differences reflect different cognitive processes involved in processing inflectional morphology in the two languages.

In this study, bilingual subjects, who were highly proficient in both languages from a young age, performed a lexical decision task in both languages. Target words were preceded by primes presented briefly and subconsciously. Morphological, semantic, and orthographic manipulations were introduced by changing the relations between the target and its primes. Two morphological conditions were used—in one, words were morphologically related but not semantically related, and in the other, the words were both semantically and morphologically related. We chose to use the masked priming paradigm (Forster & Davis, 1984) as it has been extensively used in morphological research, specifically in fMRI studies of morphology (Bick et al., 2010; Gold & Rastle, 2007). Additionally, this method reflects automatic rather than strategic processes as the subjects are unaware of the linguistic manipulation. This allowed us to identify brain regions that were sensitive to morphological relations between words and compare this effect to that caused when words were related to targets only in orthographic form, or in semantic meaning.

Our goal was to compare the activation pattern during processing morphology in Semitic languages and in Indo-European languages, using Hebrew and English. We were interested in identifying the networks involved in morphological processing, to test if both languages use the same network, and to quantify the differences in language processing in the two languages. Specifically, we investigated whether the interaction between processing morphological, semantic, and orthographic information is similar in both languages. This would indicate whether each language's morphological structure influences the way it is processed, or whether printed information is processed alike in alphabetic orthographies, regardless of significant morphological differences.

METHODS

Subjects

Twenty-seven volunteers participated in this study (12 men, ages ranging from 22 to 36 years, mean age = 26.33 years). All participants were right-handed without any neurological record or reading disorders. All subjects were early bilinguals, exposed to both English and Hebrew before they were 8 years old, and reported being highly proficient in both languages at testing. Participants gave written consent before taking part in the study and were paid for participating. Ethical approval was granted by the Hadassah Hebrew University Medical Center.

Magnetic Resonance Protocol

The BOLD fMRI measurements were performed in a whole-body 3-T Siemens scanner. BOLD contrast was obtained with a gradient-echo echo-planar imaging sequence and a standard head coil. Functional data were obtained using TR = 2 sec, TE = 30 msec, flip angle = 90°, imaging matrix = 80 × 80, FOV = 22 × 22 cm (in-plane resolution = 2.75 × 2.75 mm) and 30 slices, 3 mm each with 0.5 mm gap between slices. Slices were placed oblique to cover most of the brain. High-resolution three-dimensional spoiled gradient-echo (SPGR) anatomical sequence was performed in the same session as functional data.

Stimuli

Two hundred fifty-six (256) target words were used in the experiment (128 in Hebrew and 128 in English). Each target word was matched with a prime from one of the four conditions: (1) The prime was the morphological base from which the word was derived. In this condition, primes were morphologically and semantically related to the targets (MS). (2) The prime was the morphological base from which the word was derived or pseudoderived and was not semantically related to target (M). (3) A prime was orthographically similar to the target. In Hebrew, this was a three-letter word included in the target, which was not the

root of the word. In English, it was a real word, identical to the beginning of the target word, but not followed by a combination of letters used as a morphological suffix in English (O). (4) A prime that was semantically related to the target, but not derived from the same root or base (S). Examples of the stimuli employed in the experiment are presented in Table 1. In each language, conditions were balanced as to word length, frequency, and orthographic neighborhood density (no significant differences were found).

Because we were constrained to a reasonable length for an imaging experiment, we could not achieve a probability of .5 for a "yes" response in the lexical decision task; therefore, we employed 64 (not 128) target nonwords for each language in this experiment. As we were interested in the *difference in activation* in the different priming conditions for each language, this did not constitute a problem. Half of the nonwords were primed by a theoretically possible morphological root/stem and half were primed by a nonrelated prime.

Semantic relatedness was assessed by averaging subjective ratings. Fifty native speakers of each language judged the relatedness of each prime–target pair on a 1 (*not related*) to 7 (*strongly related*) scale. All pairs considered "semantically related" were ranked 5 and above, and all pairs considered "semantically unrelated" were ranked below 2.5. Mean ranks of semantic relatedness for each condition are presented in Table 1. As it is impossible to find targets with both a semantically related root/stem and a semantically unrelated stem, different targets appeared in the different conditions.

Experimental Setup

Stimulus presentation and recording of responses were implemented with Presentation software (www.neurobs.com/presentation). All words were visually presented via an LCD projector onto a tangent screen located inside the scanner, in front of the subject. Subjects viewed the screen through a tilted mirror. Behavioral performance was assessed during the fMRI scan using a response box.

Experimental Design

Subjects were asked if a visually presented letter string was an existing word in Hebrew/English and their response was monitored. The experiment consisted of eight runs (6:30 min each), containing one Hebrew and one English block and including four repetitions of the six conditions (4 of words and 2 of nonwords, in each language) per run. The order of the runs was balanced between subjects.

Blocks were preceded by a notice of the upcoming language, and by two practice trials, which were removed from the analyses. Conforming with the forward-masking paradigm (Forster & Davis, 1984), trials consisted of a sequence of three events: a 500-msec forward mask (#######), followed by a prime presented for 33 msec, replaced by

Table 1. Examples of Hebrew and English Stimuli

	Hebrew	Orthographic Translation	Phonetic Translation	Semantic Meaning	Length	Frequency	Semantic Relation
Semantic (S)	צחוק	cxwk	tzxok	laughter	4.88	12.9	6.31
	שמח	smx	same'ax	happy	3	26.47	
Morphologic + semantic (MS)	גישור	gyswr	gishur	bridging	5.09	16.6	6.52
	גשר	gsr	gesher	bridge	3	44.25	
Morphologic (M)	החלמה	hxlmh	haxlama	recovery	4.97	9.41	1.55
	חלם	xlm	xalam	dreamed	3	34	
Orthographic (O)	מזלג	mzlg	mazleg	fork	4.94	14.1	1.22
	מזל	mzl	mazal	luck	3	33.81	

	English	Length	Frequency	Semantic Relation
Semantic (S)	demand	7.03	34.87	5.91
	ask	4.09	113.8	
Morphologic + semantic (MS)	guilty	6.78	21.39	6.1
	guilt	4.31	78.6	
Morphologic (M)	department	6.91	51.2	*1.62*
	depart	4.22	52.33	
Orthographic (O)	start	6.78	39.96	1.67
	star	4	76.73	

the target which remained on the screen for 2000 msec. Participants were told that a series of hash marks would precede targets but no mention was made of the primes. The different trial types (6 conditions) were presented in pseudorandom order, with a fixation cross (+) presented during a variable intertrial interval to enable fMRI jittering in an event-related design. The intertrial interval range and pseudorandom ordering were customized for the present design using the optseq2 program (http://surfer.nmr.mgh.harvard.edu/optseq/) in order to achieve optimal experimental efficiency (Dale, 1999).

Data Analysis

A behavioral log file was used to identify trials with null or incorrect responses. Errors and responses longer than 2500 msec were discarded from the behavioral or imaging data analysis. Similarly, trials in which prime presentation included timing errors beyond 5 msec were excluded from further analysis as well.

Error rate (including both errors and null responses) was calculated for each subject. Within each subject, reaction times (RTs) that were outside a range of 2 standard deviations were replaced with the appropriate cutoff value. This standard procedure was used to minimize the effect of outliers. Corrected RTs were used for ANOVA.

Imaging data analysis was performed using the Brain-Voyager Qx software package (Brain Innovation, Maastricht, The Netherlands, 2000). Prior to the statistical analysis, the raw data were examined for motion and signal artifacts. Head motion correction and high-pass temporal filtering in the frequency domain (3 cycles/total scan time) were applied in order to remove drifts and to improve the signal-to-noise ratio. Significant motion was found (maximum movement of 6 pixels), but as the motion was not time locked to experimental conditions, no significant motion-related artifact was identified and no cutoff was used to discard these data. The complete dataset was transformed into Talairach and Tournoux (1988) space, Z-normalized, and concatenated.

Changes in BOLD contrast associated with the different conditions were assessed on a pixel-by-pixel basis using the general linear model (Friston, Frith, Turner, & Frackowiak, 1995) with the standard hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996). Group analyses were performed using random effect analysis. In order to correct for multiple comparisons, cluster-size threshold, based on Monte Carlo simulation ($p < .05$), was used. Morphologically related areas in the different languages were defined to be the areas showing repetition suppression, that is, a reduction in activation in the two morphological conditions relative to the orthographic and semantic conditions, and additionally showing an increase in signal during

the orthographic and semantic conditions relative to the resting condition $(([O + S] > [MS + M])$ and $([O + S] > 0))$. This was done in order to eliminate noise and include only areas involved in processing the different aspects of language.

Functional images were incorporated into the three-dimensional data sets through trilinear interpolation. The statistical parametric maps were overlaid on a cortical inflated map of a representative subject. The inflated maps were reconstructed from the T1-weighted 3-D images. The procedure included segmentation of the white matter, using a grow-region function, the smooth covering of a sphere around the segmented region, and the expansion of the reconstructed white matter into the gray matter.

Functional ROIs corresponding to morphological conditions were defined in the left inferior frontal gyrus (lIFG) and left middle frontal gyrus (lMFG) for each subject individually, using the same contrast used for defining morphological related areas in group analysis ($p < .05$, not corrected). This contrast allowed us to investigate the influence of semantic transparency on morphological processing in regions involved in morphological processing. Note that the definition of the ROIs is independent of the contrast between the morphological conditions. Activated voxels, located within 25 mm of the multisubject activity center, were defined as morphological ROIs. Such ROIs were found in 24 subjects in the MFG and in 23 subjects in the IFG. A similar method was used when processing data from each language separately: We contrasted the two morphological conditions with the other two language conditions, in conjunction with an increase in activation in the orthographic and semantic conditions in each language. In this analysis, we included also the occipital regions in the left hemisphere to allow a fuller investigation of the regions in the left hemisphere involved in morphological processing in both languages. Activated voxels located within 25 mm of that language's multisubject activity center were defined as ROIs. Such ROIs were found for Hebrew in 21 subjects in the MFG and in 23 subjects in the IFG, and for English in 25 subjects in the MFG and in 23 subjects in the IFG. In these ROIs, hemodynamic responses associated with the different conditions were estimated using deconvolution analysis (Glover, 1999). From these hemodynamic responses, averaged bar histograms for the different tasks were calculated ($t = 2$–12 sec) and were subjected to statistical analysis using paired two-tailed t tests and paired ANOVA.

RESULTS

Behavioral Results

The mean accuracy and RTs are shown in Table 2. Overall, subjects displayed adequate performance (average error rate for all priming conditions: $3.37 \pm 4.64\%$). Further statistical analysis was performed on RTs for correct trials only. ANOVA of RTs identified a main effect of language [$F(1, 26) = 28.8, p < .001$] and morphology [$F(1, 26) = 28.6, p < .001$]. No significant effect of semantics [$F(1, 26) < 1.0$] or any interaction between language and semantics [$F(1, 26) < 1.0$] or language and morphology [$F(1, 26) < 1.0$] was found, although the interaction between morphology and semantics was nearly significant [$F(1, 26) = 4.01, p < .056$]. The faster RTs for words in Hebrew probably reflect some proficiency differences between languages: Most subjects defined themselves as Hebrew dominant.

Imaging Results

Maps were calculated to identify voxels involved in unique morphological processing in both Hebrew and English. As priming usually creates repetition suppression, we expected a *reduction* in signal in the relative areas. Areas involved in morphological processing in each language were defined as those areas where activation in both morphological conditions was reduced relative to the semantic and orthographic conditions, and activation in the semantic and orthographic conditions was higher than the resting condition ($p < .001$). In both languages, the lIFG, the lMFG, and regions in the inferior temporal lobe and occipital lobe were significantly modulated by morphological priming (see Figure 1 and Table 3). As can be seen in Figure 1, the networks involved in morphological processing in Hebrew and in English highly overlap (Table 4).

In order to directly compare the activation between conditions in the different languages, we defined ROIs in the regions we previously found to be involved in morphological processing in Hebrew (Bick et al., 2010)—in the lIFG and lMFG—by identifying a common morphological network for both languages (see Methods). In all these regions, activation was reduced when targets were primed by morphologically related words compared to the orthographic and semantic conditions. This effect was found in both Hebrew and English for both semantically related (two-tailed paired contrast; IFG: Hebrew, $p < .001$; English,

Table 2. Behavioral Results, Mean Response Latencies, and Standard Errors

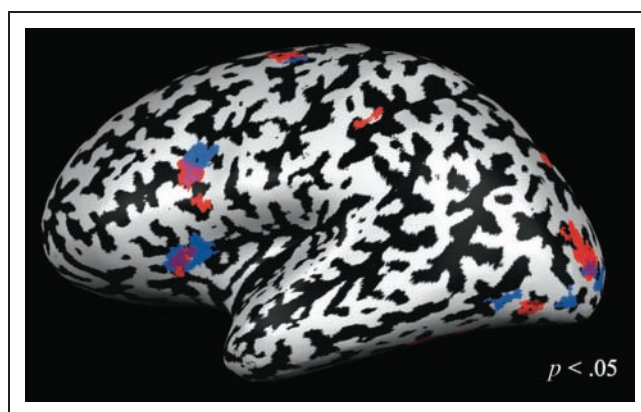|	Hebrew				English			
	S	MS	M	O	S	MS	M	O
% Error	2.6 ± 3.1	1.06 ± 1.5	1.39 ± 2.5	1.62 ± 2.5	2.35 ± 3	1.79 ± 2.3	5.66 ± 5.5	6.94 ± 5.6
Reaction time (msec)	745 ± 23	715 ± 19	719 ± 22	740 ± 20	858 ± 30	812 ± 26	827 ± 30	847 ± 31

Figure 1. Regions involved in morphological processing in Hebrew (blue) and in English (red). Regions of overlap are marked in purple.

$p < .001$; MFG: Hebrew, $p < .001$; English, $p < .001$) and semantically unrelated pairs (IFG: Hebrew, $p < .001$; English, $p < .001$; MFG: Hebrew, $p < .001$; English, $p < .001$). It is important to note that in these ROIs, no significant differences were found between the semantic and orthographic conditions in Hebrew or in English [two-tailed paired t test; IFG: Hebrew, $t(22) = 0.81$, $p < .42$; English, $t(22) = 0.24$, $p < .82$; MFG: Hebrew, $t(23) = 1.69$, $p < .1$; English, $t(23) = 1.16$, $p < .87$], ruling out the possibility that these regions are specifically involved in semantic or in orthographic processing.

We now come to the main question of our investigation, that is, is morphological processing in the two languages similar? Significant differences were found between Hebrew and English in the modulation of semantics in morphological processing. In Hebrew, in both areas, there

Table 3. Regions Showing a Morphologically Related Repetition Suppression

	BA	Mean x	Mean y	Mean z	Z at Peak Voxel	Cluster Size (mm)
Hebrew						
Left occipital–temporal	18, 19, 37	−33	−80	−6	5.57	1835
Left calcarine sulcus	17, 18	−17	−92	−6	4.67	750
Left MFG	6, 9	−35	7	29	5.52	431
Left IFG	13	−27	12	11	5.34	1646
Left precentral gyrus, left MFG	24, 6	−21	−15	45	5.18	444
Left medial frontal gyrus	6	−8	3	53	5.03	560
Right cingulate gyrus	24, 32	14	9	39	4.79	1151
Right IFG, right insula	13	33	22	13	5.59	1023
Right occipital–temporal regions	17, 18, 19	30	−84	0	6.05	5705
Right cingulate	23	17	−29	31	4.88	567
Right insula		21	2	7	4.83	368
White matter		28	−6	30	5.44	561
		−24	−18	30	5.45	423
English						
Left MFG, left IFG	44, 9, 13, 6	−43	8	18	5.99	765
Left IFG	13	−27	22	11	5.17	914
Left inferior parietal lobe	2, 40	−45	−28	39	5.43	318
Left visual regions	18, 19	−30	−82	2	5.98	2046
Left fusiform gyrus	20, 37	−31	−43	−17	5.7	793
Left MFG	6	−22	−10	49	5.53	398
Left cingulate gyrus, left medial frontal gyrus	24, 32, 6	−4	3	51	5.81	2009
Right visual regions	18, 19	28	−76	3	5.4	3607
Right insula, right IFG	13	29	21	10	5	621
Right cingulate gyrus	24, 32	9	15	31	5.48	482
Right fusiform gyrus	37	40	−50	−10	4.91	497

Table 4. Regions Where Morphologically Related Repetition Suppression in Hebrew and English Overlapped

Hebrew–English Overlap	Mean x	Mean y	Mean z	Size (mm)
Left MFG	−37	12	25	47
Left IFG	−30	20	15	179
Left visual regions	−31	−82	−3	578
Right IFG	30	23	14	185
Left SMA	−7	3	53	183
Right visual regions	32	−82	1	1057

was no significant difference between the semantically transparent (MS) and semantically opaque (M) morphological conditions [two-tailed paired t test; IFG: $t(22) = 0.98$, $p < .33$; MFG: $t(23) = 0.97$, $p < .34$], whereas in English, activation in the two morphological conditions differed significantly, with a significant decrease of activation when prime and targets were both morphologically and semantically related [IFG: $t(22) = 4.5$, $p < .005$, MFG: $t(23) = 2.54$, $p < .05$]. This differential effect of repetition suppression in the two languages was significant [IFG: $F(1, 22) = 6.046$, $p < .022$; MFG: $F(1, 23) = 6.066$, $p < .022$] (Figure 2).

To further examine this cross-linguistic difference and avoid possible confounds between the two languages, we repeated the analysis using ROIs defined for each language individually. The procedure was similar to that used for both languages together, and this time we included the regions significantly activated in the occipital region as well. Results in frontal regions showed the same pattern as before—in both languages, in all relevant areas, a significant morphological effect was found regardless of semantic transparency ($p < .001$). However, similar to the findings obtained when ROIs were defined for both languages together, a significant modulation by semantics was found in English but not in Hebrew, that is, in Hebrew, the morphological conditions did not differ [IFG: $t(22) = 0.53$, $p < .6$; MFG: $t(20) = 0.88$, $p < .39$], whereas in English, a semantic overlap between morphologically related primes and targets resulted in repetition suppression, and activation was significantly reduced relative to when primes and targets were not semantically related [IFG: $t(24) = 3.13$, $p < .005$; MFG: $t(19) = 2.34$, $p < .05$].

Occipital regions in both languages included two ROIs—one occipital region and one occipito-temporal (see Table 3). In the occipital regions involved in early visual processing, the pattern of activation was similar to that found in the frontal regions. In Hebrew, a weak morphological effect was found in the semantically opaque condition relative
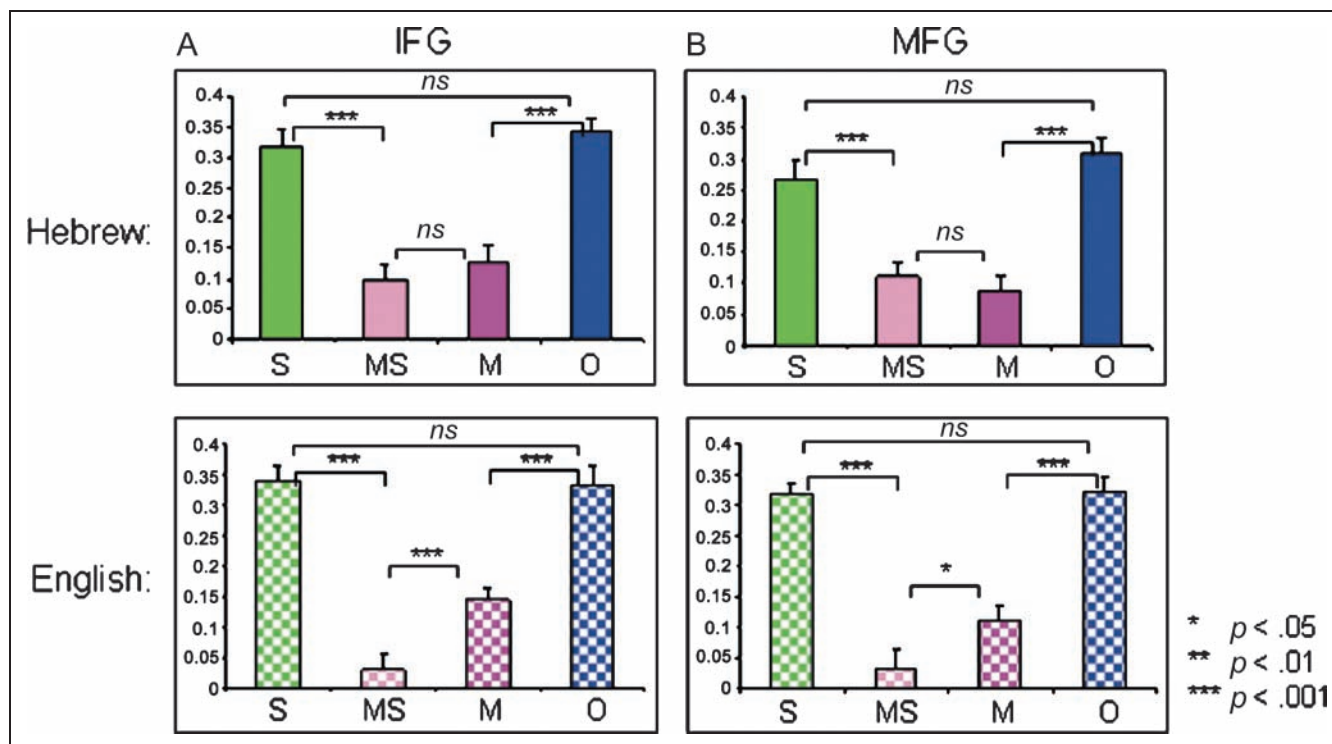

Figure 2. Activation areas showing a morphological effect in both languages. ROIs were defined as regions showing an increase in activation in the orthographic and semantic conditions, and in addition, a decrease in activation during the morphological conditions relative to orthographic and semantic conditions. For each ROI, the average beta weights 2–12 sec after presentation of stimuli were calculated for the different conditions (light pink = morphologically and semantically related prime; dark pink = morphologically and semantically unrelated prime; green = semantically related prime; blue = orthographically related prime. Hebrew is in solid blocks, English is in the squared blocks). Activation in the following regions in the left hemisphere is presented: (A) IFG; (B) MFG.
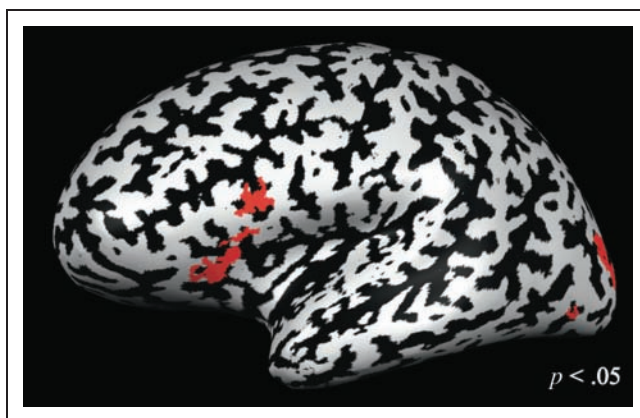
Figure 3. Areas showing both a morphological priming effect and a significant difference between the two morphological conditions in English. In Hebrew this contrast resulted in no significant cluster.

to the semantic condition ($p < .03$) and to the orthographic condition ($p < .01$). When words were semantically transparent, there was a significant reduction in signal relative to the orthographic condition ($p < .02$), but not relative to the semantic condition [$t(18) = 1.72, p = .1$]. Similar to the frontal regions, no difference was found between the morphological conditions [$t(18) = 1.19, p = .26$]. The similarity between the occipital and frontal regions is also apparent in English. A reduction was significant for both morphological conditions ($p < .001$), and a significant difference was found between them [$t(16) = 2.16, p < .05$]. As these regions are involved in processing low-level visual information, we assume this effect reflects top–down modulation caused by attention and does not reflect morphological processing.

In the occipital–temporal (OT) region, the pattern is more complex. In Hebrew, the results are similar to those found in the frontal lobe; activation in each of the morphologically related conditions was reduced relative to the other conditions ($p < .005$), and no significant difference was found between the morphological conditions [$t(16) = 0.62, p = .54$]. In English, on the other hand, similar to the frontal lobe, there was a significant morphological effect for each of the morphological conditions ($p < .001$), but unlike the frontal lobe, no significant difference between morphological conditions could be found [$t(24) = 0.86, p = .39$].

This difference between Hebrew and English is clearly seen in Figure 3: In this figure, we indicate those areas that show a morphological effect (obtained by contrasting both morphological conditions with the semantic and orthographic conditions) together with a difference between the two morphological conditions. As seen in the figure, large areas, similar in location to those identified previously to be involved in morphological processing ($p < .05$, cluster size corrected to larger than 756 mm), were obtained only for processing in English. In Hebrew, on the other hand, no significant activation was found, suggesting again that morphological activation was not modulated by

semantic transparency ($p < .05$, cluster size corrected. At lenient cluster of 108 mm, small clusters were found in the OT).

One issue to consider is the level of English proficiency of our participants. This proficiency was assessed through self-report, and our behavioral results demonstrate that although our participants were all highly proficient in English, they were, nevertheless, on the average, Hebrew dominant. The question at hand is whether language dominance has influenced our results. Our sample included 12 participants who were English dominant or fully balanced bilinguals. We therefore examined the results in the ROIs in this subgroup. Our analyses revealed an identical pattern as the full sample of participants: In both IFG and MFG a significant reduction in activation was found for both morphological conditions (IFG: $p < .002$; MFG: $p < .01$). However, although no difference in Hebrew was found between the two morphological conditions [IFG: $t(9) = 1.89, p = .09$, MFG: $t(10) = 0.6, p = .56$], a significant difference in English was found [IFG: $t(9) = 2.44, p < .05$; MFG: $t(10) = 2.4, p < .05$]. These findings suggest that language dominance did not effect our findings.

DISCUSSION

In this article, we show how the structural properties of language shape the processing of morphological information in the brain. Focusing on morphological priming, we demonstrate that although the same network is involved in processing morphology in languages such as English and Hebrew, clear cross-linguistic differences emerge in how semantic information modulates morphologically related repetition suppression in the two languages. These findings are in line with an ecological view of language processing (Frost, 2009), and impose important constraints on all current models of visual word recognition. We will now discuss our main findings and their implications for current neurobiological models of language.

First, in contrast to the findings reported by Devlin et al. (2004), the present imaging results clearly demonstrate the independent role of morphological processing. This was shown both in Hebrew and in English, two languages that have very different morphological systems. Moreover, our findings suggest that the same network is involved in processing morphological information in Semitic and in Indo-European languages: In both languages, the same areas showed a significant decrease in activation in the morphological conditions when contrasted with the semantic and the orthographic conditions.

Thus, three main areas seem to be implicated in processing morphological information: the lIFG, the lMFG, and the lOT. Our present results in the lIFG converge with our previous fMRI results in Hebrew (Bick et al., 2010), and also coincide with imaging results in English. For example, Bozic et al. (2007) found morphologically related activation within the inferior frontal lobe, independent of

semantics or orthography. The IFG has been found to be connected to morphological processing in various languages such as English (Longe, Randall, Stamatakis, & Tyler, 2007), German (Longoni, Grande, Hendrich, Kastrau, & Huber, 2005), Finnish (Lehtonen, Vorobyev, Hugdahl, Tuokkola, & Laine, 2006), and Spanish (Hernandez et al., 2004). These studies compared simple versus complex words (Laine, Rinne, Krause, Teras, & Sipila, 1999), the processing of inflected verbs and nouns (Tyler, Bright, Fletcher, & Stamatakis, 2004), and the processing of regular versus irregular verbs (Beretta et al., 2003) as well as gender judgments (Heim, Alter, & Friederici, 2005). The lMFG was shown to be involved in morphological processing in Hebrew (Bick et al., 2008, 2010), and in morphosyntactic processing in English (Shapiro et al., 2005; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005) and Italian (Marangolo, Piras, Galati, & Burani, 2006), as well as in artificial syntax (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006). (For a detailed discussion of the role of these areas in language processing in general and specifically in morphological processing, see Bick et al., 2008, 2010.)

The regions in the left OT showed a similar repetition suppression effect for both morphological conditions on both languages. The OT is known to be involved in form processing (Cohen et al., 2000, 2002; Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002; Dehaene et al., 2001). Specifically, this region was activated by explicit morphological processing (Bick et al., 2008), but activation could not be differentiated from activation during orthographic or phonological processing. Similar findings were reported by Devlin et al. (2004), and in a revised study, Gold and Rastle (2007) found in the OT a region showing morphologically repetition suppression that could not be explained by semantic or orthographic factors. Our results showing a morphological effect that is not influenced by semantics strengthen Gold's conclusions that this region is involved in the structural level of morphological processing that is mainly morpho-orthographic (see Rastle & Davis, 2008 for a detailed review). At this level, in both languages, morphological processing is blind to semantic consideration.

Cross-linguistic Differences in the Brain

Although the same areas seem to be implicated in morphological processing in the two languages, clear cross-linguistic differences emerge in what determines activation in these areas. Our main interest centered on how semantic information modulates morphological activation. Our results seem straightforward: In Hebrew, morphological processing was unaffected by the semantic properties of the stimulus, whereas in English, modulation of morphological activation by semantic processing was observed. As no semantic adaptation was found in these areas, this effect seems to result from morphological processing per se. Although our experimental design did not assess directly semantic priming effects (an unrelated condition was not

included), the semantic modulation of early morphological effects in English is in accordance with ERP studies demonstrating involvement of semantics at early stages of reading, commonly associated with orthographic and morphological encoding of English words (Penolazzi, Hauk, & Pulvermuller, 2007). They are also consistent with behavioral results showing that early morphological processing in English is morphosemantic (e.g., Feldman, O'Connor, & Del Prado Martin, 2009). However, they seem inconsistent with the common view supported by a large number of studies suggesting that morphological analysis of English words is initially morpho-orthographic, and thus, blind to semantic considerations (see Rastle & Davis, 2008 for a review). Interestingly, ERP studies also show contradictory results regarding the dependence of the morphological effect on semantics: Although some found no effect of semantic transparency (Koester & Schiller, 2008; Lavric et al., 2007), others could not clearly report an effect for semantically opaque morphologically related words (Morris et al., 2007).

In contrast to English, in Hebrew, semantics and morphology are clearly orthogonal factors. Behavioral experiments using masked priming consistently reveal that morphological effects are not modulated by the semantic relation between primes and targets (Frost et al., 1997, 2000). These findings have been reflected in parallel imaging studies with an independent processing system (Bick et al., 2008, 2010). The results of the present study clearly demonstrate that in contrast to English, the neural circuitry involved in processing morphological information in Hebrew simply does not consider the semantic overlap between primes and targets if they are morphological derivations.

The cross-linguistic differences in brain activation revealed in Hebrew versus English stem from the structural properties of the two languages. The structure of Semitic languages such as Hebrew is based on embedding roots into phonological word patterns so that almost all words are morphologically complex. Because the Hebrew lexical system is organized by root morphemes, the reader (and speaker) of Hebrew considers root information as a primary step in word recognition. The process of extracting root consonants from print or speech is a structural process blind to semantic considerations. Indeed, awareness to the root morpheme and the ability to manipulate it can be found in children from a very early age (Ravid & Malenky, 2001; Berman, 1982). In English, on the other hand, stems are words on their own, so that most words are not morphologically complex. Morphological complexity is created by appending prefixes and suffixes to base words, however, prefixes and suffixes are represented by letter clusters that often do not represent morphemes (ER in *darker* vs. ER in *corner*, or IM in *impatient* vs. IM in *impress*). Because there are no a priori rules that systematically predict when a given letter cluster is a morphemic unit, morphological relatedness is, in fact, determined, and thus, modulated by semantic considerations.

This is the essence of the ecological view of language processing (Frost, 2009). Our imaging results indeed

demonstrate that the specific linguistic properties of a given language modulate the way it is read and processed. Consequently, the neural circuitry involved in identifying words is designed to optimally process the specific properties of the linguistic environment of the reader and speaker. Hence, although some aspects of language are universal, the specific characteristics of each language must be considered in neurocognitive models of language processing. This ecological view has important implications for adapting methods of linguistic remediation or reading instruction methods from one linguistic system to another.

Most subjects participating in the experiment were bilinguals exposed to both languages at an early age. The similarity between our results for Hebrew–English bilinguals and our previous results with Hebrew speakers (Bick et al., 2010) demonstrate that even when two languages, such as Hebrew and English, are acquired in early childhood, the processing system develops for each language, given its linguistic structure. However, because results regarding English monolinguals are inconsistent, it is unclear whether our findings in English obtained with our bilingual subjects were influenced by the dominant role of morphology in their other language—Hebrew. The question of the possible interactions between the two languages in the bilingual brain has been attracting much attention in recent years (for some examples, see Chee, 2009), and additional research is necessary in order to address this question. It is important to note that if such an interaction does exist, it may be that the differences between morphological processing in Semitic languages and Indo-European languages are even greater than those revealed in this study.

In conclusion, our findings support an ecological theory of language processing. In both languages, we found morphological processing that is independent of orthography and semantics, and identical brain circuitry is involved in processing morphological information. However, the structural properties of the language modulate the way it is eventually processed. Further fine-grained research is necessary to account for the possible influence of one linguistic system on the other in the bilingual brain, to gain better understanding of how more than one language is processed in the brain.

REFERENCES

Abutalebi, J., Annoni, J. M., Zimine, I., Pegna, A. J., Seghier, M. L., Lee-Jahnke, H., et al. (2008). Language control and lexical competition in bilinguals: An event-related fMRI study. *Cerebral Cortex, 18,* 1496–1505.

Beretta, A., Campbell, C., Carr, T. H., Huang, J., Schmitt, L. M., Christianson, K., et al. (2003). An ER-fMRI investigation of morphological inflection in German reveals that the brain makes a distinction between regular and irregular forms. *Brain and Language, 85,* 67–92.

Berman, R. A. (1982). Verb-pattern alternation: The interface of morphology, syntax, and semantics in Hebrew child language. *Journal of Child Language, 9,* 169–191.

Bick, A., Goelman, G., & Frost, R. (2008). Neural correlates of morphological processes in Hebrew. *Journal of Cognitive Neuroscience, 20,* 406–420.

Bick, A. S., Frost, R., & Goelman, G. (2010). Imaging implicit morphological processing: Evidence from Hebrew. *Journal of Cognitive Neuroscience, 22,* 1955–1969.

Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience, 16,* 4207–4221.

Bozic, M., Marslen-Wilson, W. D., Stamatakis, E. A., Davis, M. H., & Tyler, L. K. (2007). Differentiating morphology, form, and meaning: Neural correlates of morphological complexity. *Journal of Cognitive Neuroscience, 19,* 1464–1475.

Chee, M. W. (2006). Dissociating language and word meaning in the bilingual brain. *Trends in Cognitive Sciences, 10,* 527–529.

Chee, M. W. (2009). fMR-adaptation and the bilingual brain. *Brain and Language, 109,* 75–79.

Chee, M. W., Soon, C. S., Lee, H. L., & Pallier, C. (2004). Left insula activation: A marker for language attainment in bilinguals. *Proceedings of the National Academy of Sciences, U.S.A., 101,* 15265–15270.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123,* 291–307.

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain, 125,* 1054–1069.

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

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,* 321–325.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4,* 752–758.

Deutsch, A., Frost, R., Pelleg, S., Pollatsek, A., & Rayner, K. (2003). Early morphological effects in reading: Evidence from parafoveal preview benefit in Hebrew. *Psychonomic Bulletin & Review, 10,* 415–422.

Devlin, J. T., Jamison, H. L., Matthews, P. M., & Gonnerman, L. M. (2004). Morphology and the internal structure of words. *Proceedings of the National Academy of Sciences, U.S.A., 101,* 14984–14988.

Diependaele, K., Sandra, D., & Grainger, J. (2005). Masked cross-modal morphological priming: Unravelling morpho-orthographic and morpho-semantic influences in early word recognition. *Language and Cognitive Processes, 20,* 75–114.

Dijkstra, A. F. J., & Van Heuven, W. J. B. (1998). The BIA-model and bilingual word recognition. In J. Grainger & A. M. Jacobs (Eds.), *Localist connectionist approaches to human cognition* (pp. 189–225). Mahwah, NJ: Erlbaum.

Feldman, L. B. (2000). Are morphological effects distinguishable from the effects of shared meaning and shared form? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 1431–1444.

Feldman, L. B., O'Connor, P. A., & Del Prado Martin, F. M. (2009). Early morphological processing is morphosemantic and not simply morpho-orthographic: A violation of form-then-meaning accounts of word recognition. *Psychonomic Bulletin & Review, 16,* 684–691.

Forkstam, C., Hagoort, P., Fernandez, G., Ingvar, M., & Petersson, K. M. (2006). Neural correlates of artificial syntactic structure classification. *Neuroimage, 32,* 956–967.

Forster, K. I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 10,* 680–698.

Friston, K. J., Frith, C. D., Turner, R., & Frackowiak, R. S. (1995). Characterizing evoked hemodynamics with fMRI. *Neuroimage, 2,* 157–165.

Frost, R. (2009). Reading in Hebrew vs. reading in English: Is there a qualitative difference? In P. McCardle & K. Pugh (Ed.), *How children learn to read: Current issues and new directions in the integration of cognition, neurobiology and genetics of reading and dyslexia research and practice* (pp. 235–253). New York: Psychology Press.

Frost, R., Deutsch, A., Gilboa, O., Tannenbaum, M., & Marslen-Wilson, W. (2000). Morphological priming: Dissociation of phonological, semantic, and morphological factors. *Memory & Cognition, 28,* 1277–1288.

Frost, R., Forster, K. I., & Deutsch, A. (1997). What can we learn from the morphology of Hebrew? A masked-priming investigation of morphological representation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23,* 829–856.

Giraudo, H., & Grainger, J. (2001). Priming complex words: Evidence for supralexical representation of morphology. *Psychonomic Bulletin & Review, 8,* 127–131.

Glover, G. H. (1999). Deconvolution of impulse response in event-related BOLD fMRI. *Neuroimage, 9,* 416–429.

Gold, B. T., & Rastle, K. (2007). Neural correlates of morphological decomposition during visual word recognition. *Journal of Cognitive Neuroscience, 19,* 1983–1993.

Heim, S., Alter, K., & Friederici, A. D. (2005). A dual-route account for access to grammatical gender: Evidence from functional MRI. *Anatomy and Embryology (Berlin), 210,* 473–483.

Hernandez, A. E. (2009). Language switching in the bilingual brain: What's next? *Brain and Language, 109,* 133–140.

Hernandez, A. E., Kotz, S. A., Hofmann, J., Valentin, V. V., Dapretto, M., & Bookheimer, S. Y. (2004). The neural correlates of grammatical gender decisions in Spanish. *NeuroReport, 15,* 863–866.

Koester, D., & Schiller, N. O. (2008). Morphological priming in overt language production: Electrophysiological evidence from Dutch. *Neuroimage, 42,* 1622–1630.

Kroll, J. F., & Stewart, E. (1994). Category interference in translation and picture naming: Evidence for asymmetric connections between bilingual memory representations. *Journal of Memory and Language, 33,* 149–174.

Kroll, J. F., & Tokowicz, N. (2005). Models of bilingual representation and processing. In J. F. Kroll, & A. M. B. De Groot (Eds.), *Handbook of bilingualism: Psycholinguistic approaches*. New York: Oxford University Press.

Laine, M., Rinne, J. O., Krause, B. J., Teras, M., & Sipila, H. (1999). Left hemisphere activation during processing of morphologically complex word forms in adults. *Neuroscience Letters, 271,* 85–88.

Lavric, A., Clapp, A., & Rastle, K. (2007). ERP evidence of morphological analysis from orthography: A masked priming study. *Journal of Cognitive Neuroscience, 19,* 866–877.

Lehtonen, M., Vorobyev, V., Hugdahl, K., Tuokkola, T., & Laine, M. (2006). Neural correlates of morphological decomposition in a morphologically rich language: An fMRI study. *Brain and Language, 98,* 182–193.

Lehtonen, M., Vorobyev, V., Soveri, A., Hugdahl, K., Tuokkola, T., & Laine, M. (2009). Language-specific activations in the brain: Evidence from inflectional processing in bilinguals. *Journal of Neurolinguistics, 22,* 495–513.

Longe, O., Randall, B., Stamatakis, E. A., & Tyler, L. K. (2007). Grammatical categories in the brain: The role of morphological structure. *Cerebral Cortex, 17,* 1812–1820.

Longoni, F., Grande, M., Hendrich, V., Kastrau, F., & Huber, W. (2005). An fMRI study on conceptual, grammatical, and morpho-phonological processing. *Brain and Cognition, 57,* 131–134.

Mahendra, N., Plante, E., Magloire, J., Milman, L., & Trouard, T. P. (2003). fMRI variability and the localization of languages in the bilingual brain. *NeuroReport, 14,* 1225–1228.

Marangolo, P., Piras, F., Galati, G., & Burani, C. (2006). Functional anatomy of derivational morphology. *Cortex, 42,* 1093–1106.

Morris, J., Frank, T., Grainger, J., & Holcomb, P. J. (2007). Semantic transparency and masked morphological priming: An ERP investigation. *Psychophysiology, 44,* 506–521.

Penolazzi, B., Hauk, O., & Pulvermuller, F. (2007). Early semantic context integration and lexical access as revealed by event-related brain potentials. *Biological Psychology, 74,* 374–388.

Rastle, K., & Davis, M. (2008). Morphological decomposition based on the analysis of orthography. *Language and Cognitive Processes, 23,* 942–971.

Ravid, D., & Malenky, D. (2001). Awareness of linear and nonlinear morphology in Hebrew: A developmental study. *First Language, 21,* 25–56.

Rodriguez-Fornells, A., Rotte, M., Heinze, H. J., Nosselt, T., & Munte, T. F. (2002). Brain potential and functional MRI evidence for how to handle two languages with one brain. *Nature, 415,* 1026–1029.

Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review, 96,* 523–568.

Shapiro, K. A., Mottaghy, F. M., Schiller, N. O., Poeppel, T. D., Fluss, M. O., Muller, H. W., et al. (2005). Dissociating neural correlates for nouns and verbs. *Neuroimage, 24,* 1058–1067.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Tan, L. H., Spinks, J. A., Feng, C. M., Siok, W. T., Perfetti, C. A., Xiong, J., et al. (2003). Neural systems of second language reading are shaped by native language. *Human Brain Mapping, 18,* 158–166.

Tyler, L. K., Bright, P., Fletcher, P., & Stamatakis, E. A. (2004). Neural processing of nouns and verbs: The role of inflectional morphology. *Neuropsychologia, 42,* 512–523.

Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. (2005). Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing. *Neuropsychologia, 43,* 1963–1974.