Imaging Implicit Morphological Processing: Evidence from Hebrew

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Abstract

■ Is morphology a discrete and independent element of lexical structure or does it simply reflect a fine-tuning of the system to the statistical correlation that exists among orthographic and semantic properties of words? Hebrew provides a unique opportunity to examine morphological processing in the brain because of its rich morphological system. In an fMRI masked priming experiment, we investigated the neural networks involved in implicit morphological processing in Hebrew. In the lMFG and lIFG, activation was found to be significantly reduced when the primes were morphologically related to the targets. This effect was not influenced by the semantic transparency of the morphological prime, and was not found in the semantic or orthographic condition. Additional morphologically related decrease in activation was found in the lIPL, where activation was significantly modulated by semantic transparency. Our findings regarding implicit morphological processing suggest that morphology is an automatic and distinct aspect of visually processing words. These results also coincide with the behavioral data previously obtained demonstrating the central role of morphological processing in reading Hebrew. ■

INTRODUCTION

Morphology concerns the internal structure of words and is reflected by systematic correlations of form (orthography, phonology) and meaning (semantics). Models of lexical organization and lexical processing provide different answers to the question of whether morphology should be regarded as a distinct level of lexical architecture. The parallel-distributed processing tripartite view of the mental lexicon, for example, focuses on patterns of activation over processing units that correspond to the orthographic, phonological, and semantic sublexical features of a word (e.g., Seidenberg & McClelland, 1989). Thus, the parallel-distributed processing approach argues that there is no level of explicit and discrete representation that corresponds to morphological units (Rueckl, Mikolonski, Raveh, Miner, & Mars, 1997). Morphological effects, according to this view, reflect a fine-tuning of the reader or speaker to the correlations that exist between the phonological, orthographic, and semantic properties of words (e.g., Plaut & Gonnerman, 2000). In contrast, the traditional "localist" representational framework typically assumes that morphemic units are explicitly represented in the mental lexicon and are involved in the processing of print (see Taft, 1994 for a discussion).

Extensive research has been conducted to examine the role of morphology in lexical structure and to determine the question of the independence of morphological processing. A wide array of behavioral experimental paradigms such as cross-modal priming (e.g., Marslen-Wilson, Tyler, Waksler, & Older, 1994), repetition priming at various lags (e.g., Bentin & Feldman, 1990), masked priming (e.g., Rastle & Davis, 2003), segment shifting (e.g., Feldman, Frost, & Pnini, 1995), monitoring of eye movements (e.g., Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003), and letter transpositions (Velan & Frost, 2007) have shown that effects of morphological structure cannot simply be reduced to shared form or shared meaning.

Recently, attempts to address this psycholinguistic question have expanded from behavioral research to neuroimaging as well. This approach typically engages subjects in explicit or implicit morphological processing and searches for distinct patterns and sites of activation that do not overlap with those involved in orthographic, phonological, or semantic processing. The results, however, do not present a clear and unequivocal picture (for a review, see Marslen-Wilson & Tyler, 2007). Devlin, Jamison, Matthews, and Gonnerman (2004) used masked priming in English and did not detect evidence of morphological processing that could not be explained by the joint effects of semantics and orthography. In contrast, Bozic, Marslen-Wilson, Stamatakis, Davis, and Tyler (2007) and Gold and Rastle (2007) did find sites of independent activation for morphological processing in English, in both masked and long-term priming. These two studies, however, differ in the extent and location of morphological activation found, which creates difficulties in interpreting their results. Several event-related potential studies have investigated the relation between morphological processing and semantics, but have again reported contradicting results

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regarding the influence of semantics on morphological effects (Koester & Schiller, 2008; Lavric, Clapp, & Rastle, 2007; Morris, Frank, Grainger, & Holcomb, 2007).

The question of whether morphological effects can or cannot be reduced to the correlation of orthography, phonology, and meaning may be language-dependent. In general, it is well accepted that some aspects of language processing are universal. However, languages do differ in their morphological structure, and significant differences in morphological effects have been found between languages. These findings suggest a graded sensitivity to morphological manipulations in languages with a rich morphological system as opposed to languages with an impoverished one (Frost, 2009; Frost, Kugler, Deutsch, & Forster, 2005).

Within this domain, research in Hebrew is particularly interesting because of the language's morphological depth. Hebrew is a Semitic language characterized by a rich and systematic morphology. Most Hebrew words are morphologically complex, as they are composed of two abstract morphemes: the root and the word pattern. Roots, in most cases, consist of three consonants, and they convey the core meaning of the word. Word patterns can be either a sequence of vowels or a sequence consisting of both vowels and consonants, and they often convey morphosyntactic information. These morphemes are not appended to one another linearly, which is the case in languages with a concatenated morphology, such as English. Rather, the consonants of the root are intertwined with the phonemes (and therefore, the corresponding letters) of the word pattern. Roots and word patterns are abstract structures because only their joint combination results in specific phonological word forms with specific meanings. These meanings cannot necessarily be predicted by analyzing the two morphemes independently, and often two derivations of the same root do not appear to be semantically related (see Frost, Forster, & Deutsch, 1997 for a detailed description of Hebrew morphology).

Behavioral studies in Hebrew have consistently demonstrated that words are automatically decomposed during word recognition, and that the triconsonantal root morpheme mediates lexical access (Velan, Frost, Deutsch, & Plaut, 2005; Frost, Deutsch, & Forster, 2000; Frost, Deutsch, Gilboa, Tannenbaum, & Marslen-Wilson, 2000; Deutsch, Frost, & Forster, 1998; Frost et al., 1997). Taken together, these studies suggest that Hebrew readers and speakers are routinely engaged in morphological decomposition that is distinct from semantic and orthographic processing. Hebrew, therefore, provides a unique opportunity to examine how the brain processes morphological information.

In a recent study, the independence of morphological processing was clearly demonstrated using an explicit task in Hebrew (Bick, Goelman, & Frost, 2008). In this study, we identified two areas, the left middle frontal gyrus (lMFG) and the left intraparietal sulcus (lIPS), which showed significantly higher activity during a task that required explicit judgments of morphological relatedness, relative to other linguistic tasks such as judgments of semantic and ortho-

graphic similarity. Furthermore, we have shown that this activation is independent of the semantic properties of the stimuli. Both the lMFG and lIPS are known to be involved in reading (e.g., Seghier et al., 2004), and specifically in grammar-related tasks (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005). For example, Shapiro, Moo, and Caramazza (2006) demonstrated differential activation in response to verbs and nouns, and Marangolo, Piras, Galati, and Burani (2006) have shown these areas to be activated in a morphological derivation task.

However, demonstrating that at relatively long time courses explicit morphological judgments can be differentiated from decisions regarding semantic and orthographic similarity may not necessarily reveal whether morphological computation is a primary process occurring in the initial stage of visual word recognition. Behavioral research thus often focuses on implicit tasks that tap early and automatic processing, which is independent of subjects' explicit strategies or the conscious awareness of the morphological manipulation. The masked priming paradigm (Forster & Davis, 1984) is particularly useful for exploring early processes of word recognition because the brief presentation of the prime combined with forward and backward masking prevents the full conscious identification of the prime. Consequently, the priming effect obtained in this procedure is not influenced by the participants' conscious appreciation of the prime–target morphological or orthographic relation, as is the case with some long-term priming effects. Masked priming has been extensively used in behavioral studies as well as in neuroimaging research. Consistent results show that priming under masked presentation modulates activation in relevant areas (for a review, see Henson, 2003). For instance, imaging studies have found that priming with semantically related words creates changes in activation in areas related to semantic processing. In some studies, however, a reduction in activity was observed whereas in others, activity increased (i.e., Devlin et al., 2004; Copland et al., 2003; i.e., Gold et al., 2006; Raposo, Moss, Stamatakis, & Tyler, 2006). The precise nature of the neuronal mechanisms involved in priming are still under investigation (James & Gauthier, 2006; Schnyer, Ryan, Trouard, & Forster, 2002). Recent studies have shown that priming effects might be strongly influenced by task (Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2007) and brain region (Wig, Buckner, & Schacter, 2009; Horner & Henson, 2008), and different hypotheses, such as cortical tuning, neural adaptation, and response learning, have been offered to account for priming effects (see Race, Shanker, & Wagner, 2008).

In the present article, we report fMRI results using implicit morphological manipulations in Hebrew. Subjects were engaged in a lexical decision task; target words were preceded by a brief and unconscious presentation of primes. Morphological, semantic, and orthographic manipulations were introduced by changing the relations between the target and its primes. 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 semantically or orthographically related to targets. Note that activity studied in this experiment is not explicitly aroused by the experimental demands, but rather implicitly elicited by the very brief presentation of the prime, thereby reflecting rapid and automatic decomposition. Our goal was twofold: first, to identify areas that are involved in early and automatic morphological processing and to provide a necessary point of comparison for our previous neuroimaging results of explicit morphological judgments in Hebrew. We were interested in finding whether both experimental procedures use the same or different networks. Our second aim was to provide a contrast to previous English studies. Because masked priming has been employed in imaging experiments in English (Gold & Rastle, 2007), using the same method in a language with a deep morphology such as Hebrew will enable us to progress in understanding the influence of morphological depth on morphological processing.

METHODS

Subjects

Twenty volunteers participated in this study (10 men and 10 women ages ranging from 18 to 31 years, mean age = 26.5 years). All participants were right-handed without any neurological record or reading disorders. Hebrew was the mother tongue of all subjects and none of them were exposed to other languages in early childhood. 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 1.5-T Siemens Avanto 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 = 50 msec, flip angle = 90°, imaging matrix = 64 × 64, FOV = 20 × 20 cm and 21 slices, 3 mm each with 1-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 preformed in the same session as functional data.

Stimuli

One hundred sixty target words were used in the experiment. Each target word was matched with five primes: (1) A prime derived from the same root as the target, with a similar meaning. Hence, this prime was morphologically and semantically related to the target (MS). (2) A prime derived from the same root but not semantically related (M). As explained above, this condition is unique to a language such as Hebrew. (3) A prime orthographically similar to the target (sharing at least three letters in the same order, but not all of the root letters, unlike the morphological primes). We refer to this condition as O. (4) A prime semantically related to the target, but not derived from the same root (S). And (5) a control prime not related to the target in any way (NR). The advantage of this within-stimulus design is that each target word served as its own control for assessing the effect of morphological relatedness. All words were common Hebrew nouns or adjectives. All words were derived from productive roots and had a three-letter root (i.e., weak roots were not employed; see Frost, Deutsch, & Forster, 2000).

Semantic questionnaires were used to control for semantic relatedness. Fifty subjects judged the relatedness of each prime–target pair on a 1 (*not related*) to 7 (*strongly related*) scale. All pairs considered "semantically related" had to have been ranked above 4.5 and all pairs considered "semantically unrelated" received a ranking of below 3.0. Mean ranks of semantic relatedness for each group of primes, of orthographic overlap (both shared letters and shared letters in the same position), and of phonological similarity (shared phonemes) are presented in Table 1B. In addition, prime conditions were balanced for word length, word frequency, and the difference in length and frequency between prime and target (examples of the stimuli in the five conditions are presented in Table 1A).

Because we were constrained to a reasonable length for an imaging experiment, we could not achieve a probability of .5 to a "yes" response in the lexical decision task, but rather employed 100 target nonwords in this experiment (as opposed to 160 target words). Sixty nonwords were created by combining an existing Hebrew root with an existing word pattern, but the result was an illegal combination that does not exist in the Hebrew lexicon (not all roots combine with all word patterns of Hebrew). For each of these target nonwords, three nonword primes were matched: (1) primes derived from the same root with a different word pattern, creating another nonexisting combination. We refer to this nonword condition as "pseudomorphological" (R–M); (2) primes that were orthographically related (R–O); and (3) primes that were not related (R–NR). An additional 40 nonword targets did not have an existing root and were created by simply changing letters in existing words ("rootless" nonwords). They were matched with two kinds of primes: (1) orthographically related (O) and (2) unrelated controls (NR). Length of nonwords and words was matched. Note that this structure of nonwords allowed us to examine some aspects of morphological processing even for nonword stimuli (Table 2).

Experimental Setup

Stimulus presentation and recording of responses were implemented with Presentation software (www.neurobs.

Table 1. Word Stimuli: Examples and Linguistic Properties

(A) Examples of Stimuli

	Hebrew	Orthographic Trans.	Phonetic Trans.	Semantic Meaning
Morphologic + semantic (MS)	צופן	**cwpn**	tzofen	code
	הצפנה	h**cpn**h	hatzpana	encryption
Morphologic (M)	צופן	**cwpn**	tzofen	code
	צפוני	**cp**wny	tzfoni	northern
Orthographic (O)	צופן	**cwpn**	tzofen	code
	צונן	**cw**nn	tzonen	cool
Semantic (S)	צופן	**cwpn**	tzofen	code
	קידוד	**ky**d**w**d	kidud	encoding
Control (NR)	צופן	**cwpn**	tzofen	code
	רקדן	**rkd**n	rakdan	dancer

(B) Properties of Stimuli

				Orthographic Relation		
	Length	Frequency	Semantic Relation	Shared Letters	Shared Letters in the Same Position	Shared Phonemes
Morphologic + semantic (MS)	5.13 ± 0.77	8.97 ± 12.99	6.12 ± 0.48	3.59 ± 0.62	1.75 ± 1.3	4.16 ± 0.94
	4.94 ± 0.81	8.59 ± 14.09				
Morphologic (M)	5.13 ± 0.78	8.97 ± 12.99	1.74 ± 0.49	3.61 ± 0.68	1.44 ± 1.12	4.06 ± 0.95
	5.14 ± 0.89	8.31 ± 12.26				
Orthographic (O)	5.13 ± 0.78	8.97 ± 12.99	1.42 ± 0.35	3.28 ± 0.51	1.47 ± 1.03	3.61 ± 0.96
	5.15 ± 0.79	6.21 ± 10.38				
Semantic (S)	5.13 ± 0.78	8.97 ± 12.99	5.76 ± 0.49	1.4 ± 0.96	0.43 ± 0.67	1.96 ± 1.36
	4.92 ± 0.83	8.01 ± 12.17				
Control (NR)	5.13 ± 0.78	8.97 ± 12.99	1.3 ± 0.25	1.03 ± 0.79	0.23 ± 0.49	1.66 ± 0.96
	4.84 ± 0.72	8.03 ± 11.1				

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 computer mouse. Subjects responded with the left index finger for "yes" responses and with the left middle finger for "no" responses.

Experimental Design

During the experiment, subjects were required to decide if a visually presented letter string was an existing word in Hebrew. 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 the target which remained on the screen until response (maximal exposure was 4000 msec). Participants were told that a series of hash marks would precede targets but no mention was made of primes. The different trial types (10 conditions: 5 of words and 5 of nonwords) 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

Table 2. Nonword Stimuli: Examples and Linguistic Properties

		Target	Orthographic Trans.	Prime	Orthographic Trans.	Shared Letters	Shared Letters in the Same Position
Nonwords with roots	M	נוגבן	nwgbn	נגובת	ngwbt	3.73 ± 0.7	1.68 ± 1.15
	O	נוגבן	nwgbn	נובחה	nwbhx	3.32 ± 0.67	1.5 ± 1.07
	NR	נוגבן	nwgbn	תקשית	tkswt	1.2 ± 1.04	0.28 ± 0.52
Rootless nonwords	O	תלירה	tlyrh	לגראה	lrg?h	3.05 ± 0.32	1.4 ± 1.32
	NR	תלירה	tlyrh	חונזג	xwnzg	0.47 ± 0.64	0.1 ± 0.3

order to achieve optimal experimental efficiency (Dale, 1999).

The experiment was divided into four runs, each containing 40 word targets (8 in each of the 5 conditions) and 25 nonword targets (5 in each of the 5 conditions) so that each run lasted about 9 min. The stimuli were divided into five lists. Each list contained 32 words and 20 nonwords in each of the five experimental conditions. The stimuli were rotated within the five conditions in each list in a Latin square design so that all targets were presented in the different conditions between subjects, but no stimulus was repeated within a subject to avoid repetition priming effects.

Data Analysis

Data analysis was performed using the BrainVoyager 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. The complete dataset was transformed into Talairach and Tournoux (1988) space, Z-normalized, and concatenated.

A behavioral log file was used to identify trials with null or incorrect responses. Responses longer than 2500 msec were considered null. All of these responses were coded as a separate condition and were not included in the analysis. Similarly, trials which included presentation timing errors beyond 3 msec were excluded from further analysis. Motion parameters calculated during motion correction for each subject were included as predictors to eliminate noise created by motion.

Changes in BOLD contrast associated with the different conditions were assessed on a pixel-by-pixel basis, using the general linear model (GLM; Friston, Frith, Turner, & Frackowiak, 1995) with the standard hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996). Group analyses were performed using random effect analysis ($p < .05$). In order to correct for multiple comparisons, a cluster size threshold was calculated for each map separately, using the BrainVoyager cluster-size

threshold plug-in, based on Monte Carlo simulation ($p < .05$). An initial mask was applied to select areas involved in global word reading. Only these volumes were included in the analysis.

Functional images were incorporated into the three-dimensional datasets 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.

Regions of interest (ROIs) corresponding to morphological conditions were defined for each subject individually by contrasting the morphological conditions with the control condition ($p < .05$, not corrected). Activated voxels, located within 25 mm of the multisubject activity center, were defined as morphological ROIs. In addition, regions corresponding to morphologically related activity identified in our previous explicit study (Bick et al., 2008) were used as an additional morphological ROI. 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 ($t = 2$–10 sec). Predictors covering the time range of 0–12 sec were used for ROI GLM contrast calculations.

Areas associated with morphological processing of words were used as ROIs for analysis of nonwords. Analysis of nonwords was identical to the analysis of words.

RESULTS

Behavioral Results

The mean accuracy and RTs are shown in Table 3. Overall, subjects displayed adequate performance (average error rate for all priming conditions: 3.22 ± 1.61%). Further statistical analysis was performed on RTs for correct trials only. ANOVA of RTs identified a main effect of lexicality ($F = 402.22$, $p < .001$). No main effect of condition was found for words ($F = 1.891$, ns). A main effect of priming condition was found, however, for the nonword stimuli

Table 3. Behavioral Results

Words	M	MS	S	O	NR	Mean Words
% Error	2.7 ± 3.7	4.4 ± 3.9	3.8 ± 4.1	3.5 ± 3.7	4.3 ± 4.7	3.8 ± 4
Reaction time (msec)	705 ± 172	685 ± 155	695 ± 161	706 ± 171	706 ± 159	700 ± 164

	With Root			*Rootless*		
Nonwords	M	O	NR	O	NR	*Mean Nonwords*
% Error	5.3 ± 6.6	8.6 ± 6.5	8.5 ± 6.3	2.8 ± 4.4	2.5 ± 6.2	5.5 ± 6.5
Reaction time (msec)	847 ± 235	851 ± 226	835 ± 208	766 ± 193	748 ± 179	808 ± 213

($p < .001$, $F = 20.6$). Planned comparisons revealed that nonwords composed of roots were rejected more slowly than nonwords that did not contain roots ($t = 8.92$, $p < .001$).

Imaging Results

Areas involved in reading were identified by contrasting all word conditions versus fixation. A most lenient threshold of .05 (corrected) was used, as to include maximum regions in the more detailed analysis. Areas identified were used as a mask, and all brain regions mentioned hereinafter are within this mask.

Maps were calculated to identify voxels involved in semantic, orthographic, and morphological processing. Results are shown in Table 4 and Figure 1. Areas involved in semantic processing were identified by contrasting the two semantic conditions [the semantically (S) and morphologically and semantically (MS) related primes] with the orthographic- and control-related primes that had no semantic relation between primes and targets. As the interaction between semantics and morphology is under debate, pure morphological primes were not used to generate this contrast. Overall, in the semantic conditions, we observed a bilateral activity increase in the middle temporal gyrus, around the left central sulcus, in the left supramarginal gyrus, left superior parietal lobe, and bilateral cuneus. A small region showing a decrease in activation was also observed in the claustrum and the insula. This pattern of activation concurs with previous results showing a pattern of both decrease and increase in activation in response to semantic priming.

Areas involved in orthographic processing were identified by contrasting the condition in which primes and targets were orthographically similar [i.e., shared at least three letters: the orthographic condition (O) and both morphological conditions (M, MS)] with the conditions in which there was no clear orthographic relation between prime and target [the semantic (S) and control (NR) conditions]. Results showed significant orthographic-related decrease in various regions in the left frontal lobe including the inferior frontal gyrus (IFG), the middle frontal gyrus, the precentral gyrus, and extending into the postcentral gyrus. Additional decrease in activation could be found in the left inferior parietal lobe and in the bilateral precuneus. Note, however, that both orthographic and semantic effects were calculated using the morphological conditions, hence, their maps may also include, to some extent, areas involved in morphological processing.

We were mostly concerned, however, with morphological processing. We therefore contrasted morphologically related activity [morphological (M) and morphological and semantic (MS) conditions] with morphologically unrelated activity [semantic (S), orthographic (O), and control (NR) conditions]. Using this contrast, a decreased fMRI signal was observed in the left IFG, in the lMFG, and in two regions in the left inferior parietal lobe (lIPL): one in the angular gyrus (AG) and the other around the IPS (see Table 3). In all of these areas, the morphological effect was found bilaterally but, to a stronger extent, in the left hemisphere (Table 4).

In order to compare temporal signal intensity between conditions, hemodynamic curves for each condition were calculated using deconvolution in the areas identified to be involved in morphological processing. Bar histograms were calculated including the average of the first seven components of the result of the deconvolution, covering 14 sec from stimuli (see Figure 2). This analysis revealed a significant reduction in activation for each of the morphological conditions in the lIFG (M vs. O + S + NR: $p < .001$; MS vs. O + S + NR: $p < .001$) and in the lMFG (M vs. O + S + NR: $p < .001$; MS vs. O + S + NR: $p < .001$). In contrast, in the parietal lobe, decrease in activation was significant only when prime and target were not semantically related (lIPS: M vs. O + S + NR: $p < .001$; MS vs. O + S + NR: $t = 1.246$, *ns*; lAG: M vs. O + S + NR: $p < .001$; MS vs. O + S + NR: $t = 0.71$, *ns*). In all of these areas, activation in the orthographic or semantic conditions did not differ significantly from activation in the unrelated conditions, suggesting that the morphological effect cannot be explained by the orthographic or semantic properties of the stimuli.

To further validate these results, signal intensities between conditions in ROIs defined in the lIFG and lMFG

were compared. ROIs were defined for each subject individually by contrasting the morphological conditions with the control condition (see Methods section). Note that because significant decrease in activation was observed only for one of the morphological conditions, no ROI was used in the parietal lobe. An across-subjects paired *t* test in these ROIs revealed a significant reduction in activation during each of the morphological conditions relative to the semantic and orthographic conditions (notice that these conditions were *not* used in defining the ROIs). Activation during the MS condition was significantly less than in the semantic condition (lIFG: $p < .0001$; lMFG: $p < .0001$) and in the orthographic condition (lIFG: $p < .0001$; lMFG: $p < .0001$). A similar result was obtained when morphologically related words were not semantically related—activation during the M condition was significantly less than in the semantic condition (lIFG: $p < .0001$; lMFG: $p < .0001$) and in the orthographic condition (lIFG: $p < .0001$; lMFG: $p < .0001$).

Explicit vs. Implicit Activation

In order to compare activation during explicit morphological processing (Bick et al., 2008) to the findings of the present study during implicit morphological processing, we overlaid the maps from the two separate studies and used the areas identified in the explicit task as ROIs for the present implicit task (Figure 3). In the lMFG, there was a clear and strong overlap between the area activated during the explicit task and the area showing morphologically related decrease in activation in the implicit task. Furthermore, in the ROI, defined by the explicit task, there was significant signal reduction during the morphological conditions relative to the other conditions (M vs. O + S + NR: $p < .001$; MS vs. O + S + NR: $p < .031$, using the second and third deconvolution components corresponding to the peak of activation). Although both tasks activated areas in the parietal lobe, overlaying the maps shows that these areas do not overlap. This is reflected in the ROI analysis as well: no significant morphologically related modulation could be found in this area (M vs. O + S + NR: $t = 1.43$, *ns*; MS vs. O + S + NR: $t = -0.12$, *ns*).

Analysis of Nonwords

We used the network involved in morphology (previously defined for words) as ROIs for the nonword data, revealing a strong morphological effect for nonwords in these areas as well. In all of these regions, activation was significantly larger when nonwords were constructed from a legal root (lIFG: $p < .0001$; lMFG: $p < .0001$; lIPS: $p < .002$; lAG: $p < .02$), suggesting the involvement of these areas in morphological decomposition aimed at extracting the root morpheme. Additionally, in the frontal areas and lIPS, activation was largest when nonwords were primed by nonwords that shared the same root: in the

lIFG (morphology–orthography: $p < .016$; morphology–control: $p < .005$; orthography–control: $t = 0.73$, *ns*), in the lMFG (morphology–orthography : $p < .005$; morphology–control: $p < .001$; orthography–control: $t = 1.04$, *ns*), and in the lIPS: (morphology–orthography: $t = 1.862$, *ns*; morphology–control: $p < .005$; orthography–control: $t = 0.907$, *ns*) whereas no significant orthographic priming effect was found in these regions. Note that whereas for words the morphological relation between prime and target caused a reduction in activation (i.e., adaptation), the morphological effect for nonwords caused an increase in activation (Figure 4).

Relation between Behavioral Results and Imaging Results

Unlike previous studies (Frost, Deutsch, & Forster, 2000; Frost, Deutsch, Gilboa, et al., 2000; Deutsch et al., 1998; Frost et al., 1997), we did not obtain the typical root prime facilitation for words. Note, however, that the number of subjects in our study is too small for obtaining reliable behavioral effects. Moreover, the conditions in the magnet are different than those in the laboratory, and the overall response latencies are not only significantly longer but also involve greater error variance. We should thus exert extreme caution in discussing the significance of the behavioral data. A subject-by-subject analysis of behavior performance revealed that half of the subjects showed a morphological priming effect (i.e., a reduction in RT in both morphological conditions relative to the other three conditions, regardless of semantics), and half did not. Therefore, we divided the subjects into two groups: one with a behavioral morphological effect and the other without. To statistically verify the validity of this division, we conducted a two-way ANOVA of behavioral data with prime condition and subject-group as fixed factors. The ANOVA, indeed, demonstrated that the interaction of group and condition was significant ($F = 4.744$, $p < .001$), with one group showing, as expected, a significant morphological priming effect ($F = 11.579$, $p < .005$), with no significant effects of semantics or orthography. Our aim in this latter analysis was to understand the relationship between behavioral and imaging effects. We therefore compared the imaging results of the two groups. The striking finding is that activation maps for both groups were similar and no significant difference was found in morphologically related areas between the groups (lIFG: $t = 0.271$, *ns*; lMFG: $t = 1.348$, *ns*; lIPS: $t = -0.759$, *ns*; lAG: $t = -0.091$, *ns*). This finding suggests that the morphologically related decrease in activation may be independent of behavioral effects and perhaps more directly reflects morphological processing. We will refer to this, at length, in the discussion below.

The greater activation for nonwords created from existing roots was correlated with an increase in response latencies in these conditions. Because for the word stimuli these areas were not tuned to task difficulty, it is unlikely

Table 4. Activations Modulated by Priming ($p < .05$, Corrected)

	Brodmann's Area	Mean x	Mean y	Mean z	Z at Peak Voxel	Cluster Size (mm)
Orthographic						
lMFG and some lIFG**	9	46	14	30	4.57	1459
L Precentral (extending to lIFG)*	44, 45, 6	53	9	7	4.15	923
L Cingulate, L superior frontal gyrus (lSFG), bilateral MFG	32, 6, 8	1	19	46	3.75	491
lIPL, L superior parietal lobe (lSPL), precuneus	40, 7	34	−49	47	3.42	696
lIPL	40	40	−42	49	3.24	309
lIFG lMFG	46, 10	39	34	11	4.51	318
L Postcentral, L precentral*	44, 9, 3, 45, 6, 4	54	−4	36	3.98	1122
L Postcentral gyrus, L precentral gyrus	2, 3, 4	58	−20	37	3.4	507
R Precuneus	7	−21	−64	39	3.95	269
R Cuneus, precuneus	7, 19	−23	−76	30	3.72	386
Semantic—Decrease in Activation						
L Claustrum, L insula	13	31	17	10	−4.03	289
Semantic—Increase in Activation						
L Superior temporal gyrus (lSTG)	22	56	2	4	3.34	302
L Postcentral, L precentral	43	60	−6	13	3.81	276
L Precentral, L postcentral	3, 4, 43	55	−10	24	4.31	323
L Postcentral, L precentral*	3, 4	45	−18	40	4.35	1161
rMTG	21, 22	−51	−31	2	4.21	361
lMTG*	21, 22	58	−42	4	4.45	447
Cerebellum		−2	−44	−12	3.76	463
lIPL, L supramarginal gyrus	40	47	−45	36	3.66	512
L Cingulate, L precuneus	31, 7	12	−44	46	2.98	272
Cuneus	17, 18	4	−78	15	4.2	668
lSPL	7	31	−64	49	3.12	298
L Middle occipital gyrus	18	28	−84	5	3.29	414
R Cuneus**	18	−12	−76	24	5.22	442
R Cuneus	19	−23	−83	32	3.57	325
Morphological Task						
lIFG, claustrum, lMFG**	45, 13, 46	37	24	11	5.26	1810
lMFG, lIFG**	9	45	13	30	4.23	2065
L Cingulate	24, 31	12	−3	46	4.59	289
lIPS	40	38	−45	43	3.22	358
lAG*	39	32	−54	34	3.98	503
L Precuneus	31, 7	19	−62	29	3.95	395
R Precuneus, lSTG, lSPL*	39, 7, 19	−26	−60	33	4.86	832

Table 4. (*continued*)

	Brodmann's Area	Mean x	Mean y	Mean z	Z at Peak Voxel	Cluster Size (mm)
R Precuneus, rSPL	7	−26	−49	51	3.24	291
rIFG, rMFG, r precentral*	9, 6	−38	9	31	4.41	1495
R Claustrum*		−31	4	−4	4.03	301

*Voxels in cluster are significant at $p < .02$.

**Voxels in cluster are significant at $p < .01$.

that task difficulty can explain the observed effect. Nevertheless, to eliminate this possibility, we calculated, for each subject, the correlations between response latency and activation in the defined ROIs. No significant correlation was found in any of the ROIs for nonwords with roots (average correlations—MFG: $r = 0$; IFG: $r = -.1$; AG: $r = -.1$; IPS: $r = -.2$) and without roots (MFG: $r = 0$; IFG: $r = -.1$; AG: $r = -.2$; IPS: $r = 0$). This analysis clearly shows that to the extent that RT reflects task difficulty, it cannot explain the morphological effect we obtained for nonwords.

DISCUSSION

In this article, we demonstrate the independent role of morphological processing by revealing morphologically specific brain activation during Hebrew reading. The unique feature of Hebrew morphology is that most words are morphologically complex, and that morphological and semantic relatedness can be manipulated orthogonally. More importantly, behavioral studies have consistently shown that visual word recognition in Hebrew routinely involves processes of morphological decomposition. Similar to Bick et al. (2008), we identified a network corresponding to morphological activity that is distinct from semantic and orthographic activity. However, although previously we focused on explicit and, perhaps, late morphological acti-

Figure 1. Statistical parametric map of 20 subjects using random effect GLM analysis ($p < .05$, cluster size corrected) for the different conditions. The three maps overlaid (green = semantic; blue = orthographic; pink = morphological) on an inflated brain of one subject, presented from a lateral view.

vation, in the present study, we extend our findings to implicit morphological processing in very early time courses of activation.

Implicit and explicit processes involve networks that partially overlap. The differences and similarities of these networks have been demonstrated for a wide range of cognitive processes (Voss & Paller, 2008; Scheuerecker et al., 2007). In the language domain, explicit and implicit processing have been investigated in studies that focused on semantic (Ruff, Blumstein, Myers, & Hutchison, 2008; Noppeney & Price, 2002) and on syntactic processing (Suzuki & Sakai, 2003).

We have found that implicit morphological processing involved bilateral fronto-parietal networks, although stronger and more robust effects were observed in the left hemisphere (for involvement of the right hemisphere in morphological processing, see Marangolo et al., 2003). The lMFG area was shown to be involved in both explicit and implicit tasks. In this area, priming by morphologically related primes resulted in significant decrease in activation. Thus, activation in the morphological conditions was significantly lower than activation of targets primed by semantic, orthographic, or unrelated primes. These morphological effects were consistent and systematic, regardless of the semantic overlap between primes and targets, suggesting that decrease in activation resulted from the common morphological properties and not from the similarity in semantic features. Consequently, and in line with our previous results, we suggest that the lMFG area is involved in the processing of morphology during reading. This conclusion is in accordance with findings showing that the lMFG area is involved in differential activation to verbs and nouns (Shapiro et al., 2006), in grammar-related tasks (Forkstam et al., 2006; Tyler et al., 2005), and in morphological derivation tasks (Marangolo et al., 2006). Therefore, the involvement of the lMFG area in morphological processing seems robust and is not task specific.

The lIFG area showed similar effects of a decrease in activation in response to morphological priming. This finding is consistent with Bozic et al. (2007), who showed morphologically related adaptation using delayed repetition priming in this area. Stronger activation in the lIFG was also found for inflected Finnish words compared with morphologically simple words (Lehtonen, Vorobyev, Hugdahl, Tuokkola, & Laine, 2006; Laine, Rinne, Krause, Teras, & Sipila, 1999), and for inflected English verbs compared with
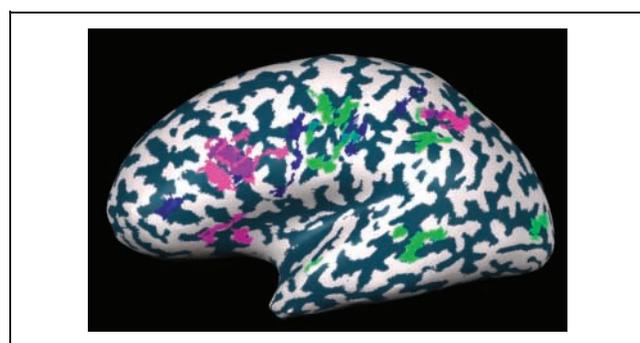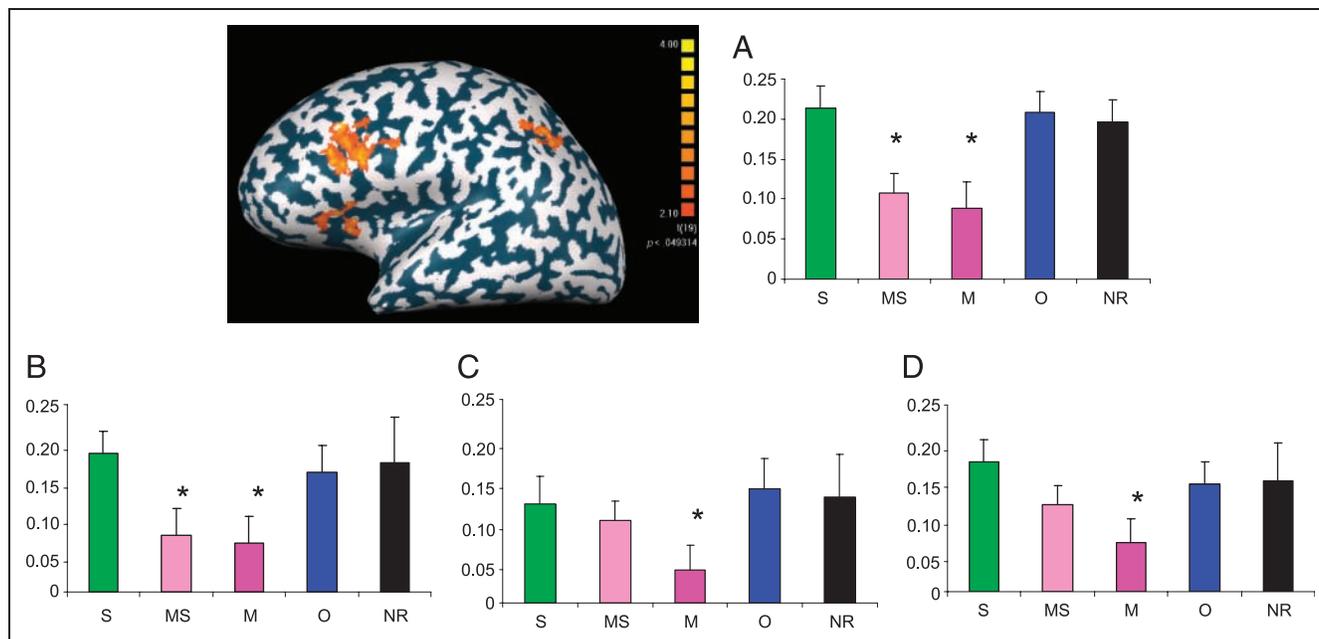
Figure 2. Areas showing morphologically related decrease in activation: ROIs were selected from multisubject maps using random effect GLM analysis ($p < .05$, corrected), contrasting both morphological conditions with other conditions (semantic, orthographic, and not related). For each ROI, the average 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; black = non-related prime). Activation in the following regions in the left hemisphere is presented: (A) lIFG; (B) lMFG; (C) lAG; (D) lIPS. Significant differences are marked ($p < .001$).
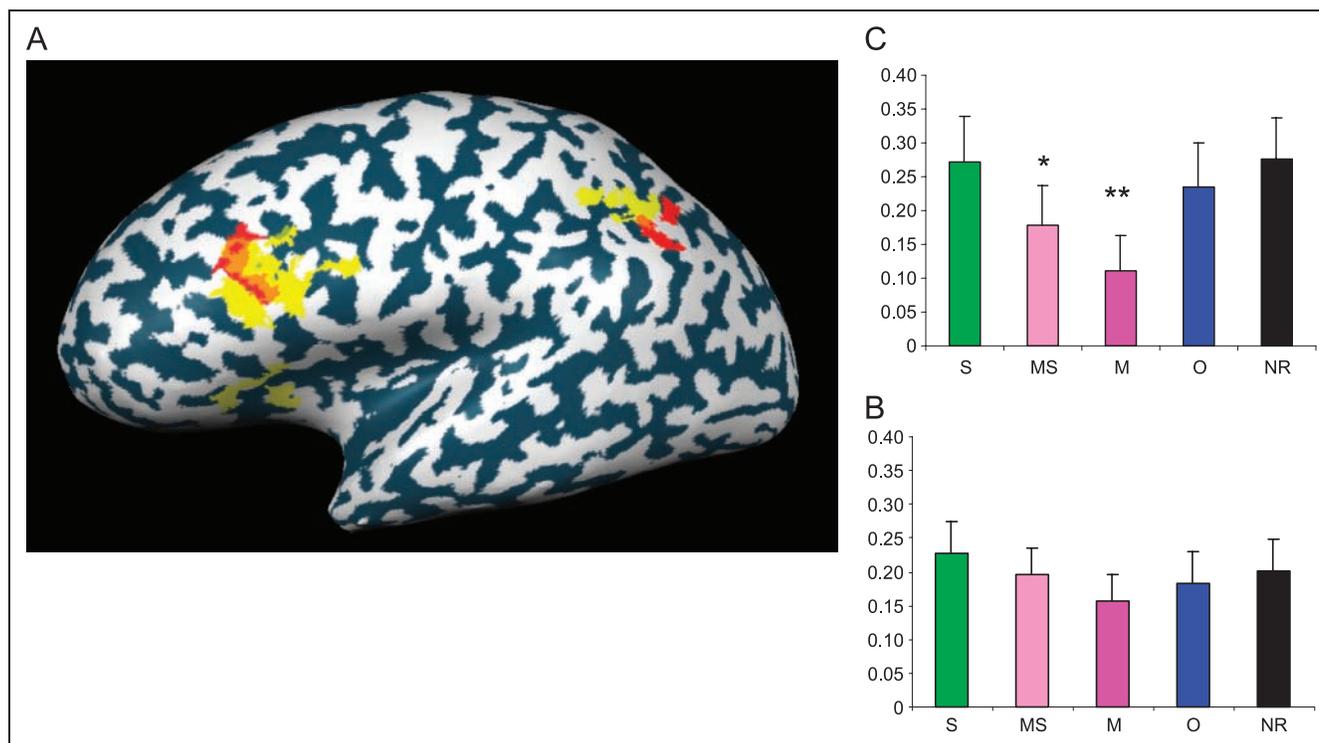
Figure 3. Relation between explicit and implicit morphological processing. (A) Regions activated by explicit (red) and implicit (yellow) morphological processing. The regions activated by the explicit tasks were used as ROIs for the implicit task. (B) Activation in the lIPS. (C) Activation in the lMFG.
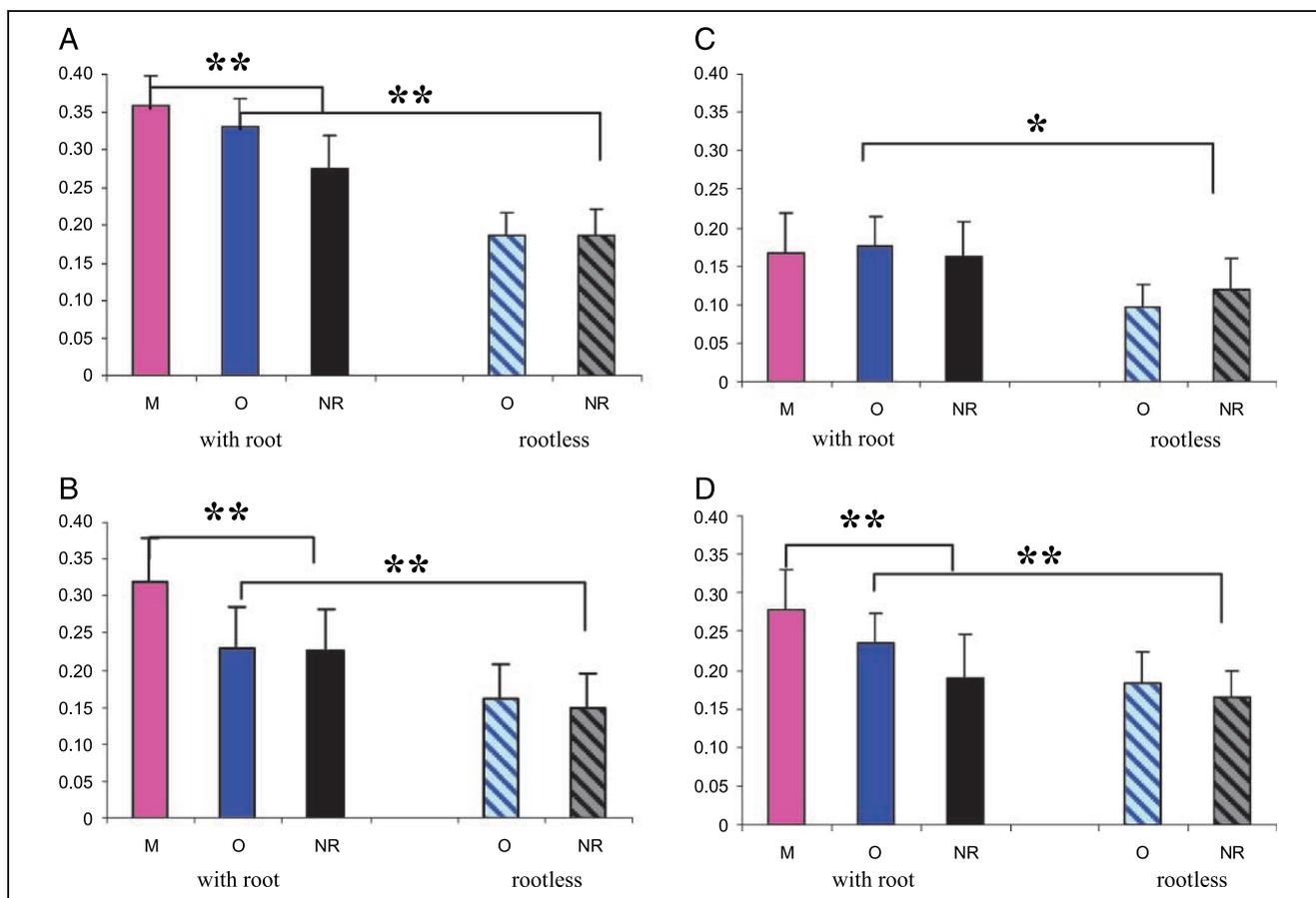
Figure 4. Activation for nonword conditions in ROIs defined for word conditions. (A) lIFG; (B) lMFG; (C) lAG; (D) lIPS. In all regions, activation for nonwords created from an existing root was significantly higher than for rootless nonwords. Furthermore, in all regions except lAG, when the prime was morphologically related, activation was significantly increased.

inflected nouns (Longe, Randall, Stamatakis, & Tyler, 2007; Tyler, Bright, Fletcher, & Stamatakis, 2004). Similarly, the lIFG area was differentially activated for regular versus irregular verbs, although the direction of the effect was inconsistent (Tyler et al., 2005; Beretta et al., 2003). The involvement of the lIFG in morphosyntactic processing is also revealed in studies of grammatical gender representation showing that when morphology was used to retrieve gender information, the superior and posterior portion of BA 44 was activated, as well as BA 45/47. In contrast, when morphology did not aid grammatical gender judgment, the activation was focused in the inferior tip of BA 44 (Heim, Alter, & Friederici, 2005; Longoni, Grande, Hendrich, Kastrau, & Huber, 2005; Hernandez et al., 2004; Fiebach, Friederici, Muller, von Cramon, & Hernandez, 2003; Miceli et al., 2002). These imaging results are consistent with neuropsychological investigations (Shapiro & Caramazza, 2003) and TMS suppression (Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001) studies of grammatical category. But note that this area was not identified in our previous explicit task. Although it was activated during explicit morphological processing, this activation was not significantly different than that found in other linguistic tasks.

Based on these findings, we suggest that the lIFG area may be involved in early and automatic morphological processing. Such processes, being automatic, take place during reading *regardless* of task, and therefore, were not modulated significantly by the different explicit judgments, which were required from the subjects in the Bick et al. (2008) study. That is, because all conditions reported by Bick et al. included real words, and because morphological decomposition occurred automatically for any Hebrew word in the lIFG, some morphological activation was probably present for all experimental conditions, and therefore, no reliable differences were found between the tasks.

Confusing results were obtained for the left parietal lobe. First, the locus of explicit activation did not overlap with the present implicit activation. More importantly, the morphological effect obtained in the lIPL was significant only for words that were morphologically related and semantically unrelated, whereas only a nonsignificant trend was revealed for words that were both morphologically and semantically related. At present, we cannot ascertain whether this outcome should be attributed to problems of statistical power in the M+S+ condition, or whether it reflects the masking of two contrasting effects: an increase of activation due to semantic priming

and a decrease in activation due to morphological priming. One possible explanation may emerge from the nature of the lIPL. The lIPL is task sensitive, and it has been specifically shown, using TMS (Nakamura et al., 2006), that the lIPL was not involved in priming when the task was lexical decision but was essential when the task required word naming. The lIPL area is known to be involved in other demanding language tasks such as complex interactions between semantics and phonology (Frost, Mencl, et al., 2005), or grammar-related tasks (Forkstam et al., 2006; Tyler et al., 2005), and is known to be sensitive to sentence complexity (Constable et al., 2004). This pattern may explain the strong involvement in explicit morphological processes, and to a less extent, in implicit morphological processing. Additional studies will be required to understand the involvement of the parietal regions in morphology.

Considering our results for both implicit and explicit tasks, we propose the following fronto-parietal network involved in morphological processing during Hebrew reading. The lIFG is involved in early and automatic morphological decomposition. This area is activated in reading and its involvement is task independent. The lMFG is not constrained to early and automatic processing and, therefore, is involved in more general aspects of morphological processing. This activation exists during reading as demonstrated by the implicit task, but is modulated by explicit morphological judgments as demonstrated in the explicit morphological experiment. The parietal lobe seems to be involved in morphological processing as well, but this involvement depends on the task and its role, so far, is unclear.

Supporting evidence for our proposed network for morphological processing is provided by the nonword data. Areas involved in morphological processing were more strongly activated when nonwords were composed of legal roots, and the strongest activation was revealed when both primes and targets shared a root. Note that because the ROIs for the nonword analyses were defined using only the words, the nonword analysis was not biased in terms of the definition of the regions. As nonwords are not represented in the lexicon, the priming effect for nonwords resulted in an increase in activation—the opposite effect than that observed for words. Although information regarding the root of a word aids its recognition and can often create a facilitatory effect, information regarding the root of a nonword supplies false and misleading information, creating an increase in activation and making it harder to reject the nonword (as expressed in Behavioral Results). The nonword data support previous behavioral results in Hebrew showing that roots are automatically extracted even for nonwords, at least when it comes to verbs (Deutsch et al., 1998). Previous cognitive studies have argued that root extraction is the initial process of reading in Hebrew and that roots serve as an organizing principle in the mental lexicon (Frost, 2009; Frost, Kugler, et al., 2005; Deutsch et al., 2003). The stronger ac-

tivation we found for nonwords derived from legal roots suggests that a root was, indeed, recognized and extracted from these printed stimuli. Furthermore, these results show that the root morpheme is, indeed, represented in the lexicon as previously suggested (Frost et al., 1997).

Overall, our results demonstrate that morphological processing is an independent process in visual word recognition. Hebrew speakers seem to activate the morphological network not only when explicitly requested to attend to morphological properties of words but also when the relation of primes and targets is not consciously perceived. These brain activation results coincide with Frost, Kugler, et al.'s (2005) previous behavioral research showing that while reading Hebrew, the root morpheme is extracted and processed, and this processing is early and automatic. This processing occurs for nonwords as well as for words, exhibiting the important part that the root plays in the organization of the Hebrew lexicon.

Is this network language-dependent? Hebrew is perfect for studying morphological processing due to its systematic and complex morphological system. As previously described, several studies demonstrated the involvement of the lIFG in morphological processing in different Indo-European languages (i.e., Lehtonen et al., 2006; Beretta et al., 2003), and this involvement was shown to be independent of orthographic and semantic processing (Bozic et al., 2007). However, because this effect was not found or replicated in a parallel study (Gold & Rastle, 2007), further research is required to unravel the processing of morphology in languages with more impoverished morphology. In the lMFG and lIPL, evidence for morphological processing was found in Indo-European languages as well, as in Hebrew, but in Indo-European languages, it is not evident that this activation is a result of morphological processing and not of other linguistic process such as semantics and orthography. Therefore, the results from Hebrew provide, for the first time, a systematic description of the areas involved in morphology, and future research is necessary to understand the relationship between morphological processing in the brain and the morphological structure of a given language.

Morphologically related decrease in activation was found both for subjects showing a behavioral effect and for subjects showing no clear consistent behavioral morphological effect. Similarly, for nonwords, morphological priming caused an increase in activation, although no behavioral effect was found. These results demonstrate the advantage of imaging techniques that can identify processes that are not reflected by behavioral measures of RT. Behavioral measures reflect the sum of all processes taking place, and other processes may mask the facilitation created by morphological priming. The advantage of imaging is that it enables focusing on the areas involved in morphological processing alone, thus separating morphological processing from other parallel processes taking place in the human brain. Furthermore, this result shows that the observed effect reflects the differences in processing

of the words induced by the different prime conditions rather than behavioral differences having to do with response execution.

In conclusion, converging evidence from explicit and implicit morphological processing clearly demonstrates that morphological processing is distinct from semantic and orthographic processing, at least in a language such as Hebrew. Our results show that morphological decomposition is early and automatic, demonstrating the central role morphology plays in reading Hebrew. The fronto-parietal network we identified is activated by morphology, regardless of the semantic properties of words, and its activation is modulated by root information even for nonwords. Additional research will be necessary to fully describe the network and its dynamics.

Acknowledgments

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