Neural Correlates of Morphological Processes in 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 the orthographic and semantic properties of words? Imaging studies in English failed to show unequivocal morphological activation that is distinct from semantic or orthographic activation. Cognitive research in Hebrew has revealed that morphological decomposition is an important component of print processing. In Hebrew, morphological relatedness does not necessarily induce a clear semantic relatedness, thus, Hebrew provides a unique opportunity to investigate the neural substrates of morphological processing. In this functional magnetic resonance imaging study, participants were required to perform judgment tasks of morphological relatedness, semantic relatedness, rhyming, and orthographic similarity. Half of the morphologically related words were semantically related and half were semantically unrelated. This design was chosen to induce explicit morphological processing. We identified two locations involved in morphological processing: the left middle frontal gyrus and the left inferior parietal sulcus. Comparing locations of morphological related activation to the locations of semantic and orthographic related activation, we found that the areas neighbored but only partially overlapped. The similarity in activation between the two morphological conditions eliminates the possibility that morphological activation simply results from the semantic properties of the words. These results demonstrate the important role of morphological processing in reading and suggest that morphological analysis is a distinct process of visual word recognition. ■

INTRODUCTION

Models of visual or auditory word perception assume that the dynamic processes involved in word recognition operate on a mental lexicon, which contains the basic linguistic units of a language. Words, in general, have phonological, orthographic, and semantic properties. However, they cannot be fully described without reference to their morphology as well. Because 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.

For example, the Parallel-Distributed Processing (PDP) tripartite view of the mental lexicon (e.g., Seidenberg & McClelland, 1989) focuses on patterns of activation over processing units that correspond to the orthographic, phonological, and semantic sublexical features of a word. Thus, the PDP approach argues that there is no level of explicit and discrete representation that corresponds to morphological units. All that can be said is that a level of hidden units picks up the correlations between phonology and semantics or orthography and semantics (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 (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. This necessarily implies that the relevant morphemes are extracted during visual word recognition (see Taft, 1994 for a discussion).

In the last decade, extensive research has been conducted to examine the role of morphology in lexical structure. The common strategy was to assemble behavioral data demonstrating that effects of morphology cannot be reduced to shared form or shared meaning. For example, it has been demonstrated that morphological priming remains robust while orthographic priming is not (e.g., Feldman, 2000). In the same vein, morphological priming effects were shown to be independent of the semantic similarity between primes and targets (e.g., Rastle, Davis, & New, 2004). These findings involved a wide array of experimental paradigms such as cross-modal priming (e.g., Marslen-Wilson, Tyler, Waksler, & Older, 1994), repetition priming at various lags (e.g.,

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Bentin & Feldman, 1990), masked priming (e.g., Rastle & Davis, 2003), segment shifting (e.g., Feldman, Frost, & Pnini, 1995), or the monitoring of eye movements (e.g., Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003).

In different languages, however, different principles govern morphological complexity. In recent years, the empirical investigation of morphological processing has, therefore, generated extensive cross-linguistic research that was based on the theoretical stance that the mapping of cognitive events involved in the recognition of morphologically complex words should depend on the linguistic environment of the native speaker. The distinct role of morphology in lexical organization was consequently demonstrated in languages such as French (Giraudo & Grainger, 2001), Dutch (Diependaele, Sandra, & Grainger, 2005), Spanish (Allen & Badecker, 2002), Italian (Laudanna, Burani, & Cermele, 1994), and Finnish (Bertram, Laine, Harald Baayen, Schreuder, & Hyona, 2000).

Within this domain, research on Hebrew morphology has been attracting significant attention because, as a Semitic language, Hebrew has a rich, complex, and systematic morphology, where almost all words are morphologically complex. In Hebrew most words can be decomposed into two abstract morphemes: the root and the word pattern (*Mishkal*/*Binyan*). Roots, in most cases, consist of three consonants, whereas word patterns can be either a sequence of vowels or a sequence consisting of both vowels and consonants. Roots and word patterns are abstract structures because only their joint combination results in specific phonemic word-forms with specific meanings. The most salient feature of Semitic languages' morphology concerns the special manner with which morphemic units are combined to form morphological complexity. In contrast to Indo-European languages where morphological complexity (inflectional or derivational) is created by a linear and sequential concatenation of morphemic units such as prefixes, stems, and suffixes, roots and word patterns in Hebrew are not appended one to the other linearly; rather, the consonants of the root are intertwined with the phonemes (and therefore, the corresponding letters) of the word pattern.

Another important characteristic of Hebrew morphology is the apparent dissociation between morphology and semantics. Although the root morphemes carry a specific semantic meaning, not all words from the same root are necessarily semantically related. This is because there is no systematic manner to obtain a given semantic meaning by combining roots with word patterns. For example, the words TARGIL (exercise), REGEL (foot), HERGEL (habit), and MERAGEL (spy) are all driven from the same root (R-G-L, which refers to anything related to foot action). Although one can trace through historical research the linguistic factors which were the origin of these derivations, clearly, they do not share a salient common meaning in modern Hebrew. As to the word pattern morpheme, in most cases, it does not express a consistent semantic meaning either and mainly conveys morphosyntactic information. This feature is unique to Semitic languages.

Behavioral studies in Hebrew have revealed that the tri-consonantal root morpheme mediates lexical access and serves as an organizing unit in the mental lexicon of Hebrew speakers. Using masked priming and cross-modal priming to examine the role of roots in Hebrew, Velan, Frost, Deutsch, and Plaut (2005), Frost, Deutsch, and Forster (2000), Frost, Deutsch, Gilboa, Tannenbaum, and Marslen-Wilson (2000), Deutsch, Frost, and Forster (1998), and Frost, Forster, and Deutsch (1997) found that root primes facilitate both lexical decision and the naming of target words derived from the same root. Regarding the dissociation of morphological and semantic processing, these studies have demonstrated that strong and robust morphological priming can be obtained even when there is no apparent semantic association between the root derivations, such as the case of TARGIL (exercise) and MERAGEL (spy). When the stimulus onset asynchrony between prime and target is long enough, however, stronger priming was obtained when morphologically related words were also semantically related (Frost, Deutsch, Gilboa, et al., 2000). Recently, Frost and his colleagues have also shown that, in contrast to English, masked form-orthographic priming effects in Hebrew are weak and unreliable, whereas masked morphological priming is always strong and robust (Frost, Kugler, Deutsch, & Forster, 2005). These findings suggest that lexical organization in Hebrew follows morphological principles, as words seem to be clustered together by root families. The difference in reading Hebrew and English is also demonstrated by measuring parafoveal preview benefit. Studies in English have demonstrated that orthographic information is extracted from the parafovea (Inhoff, 1989; Rayner, Well, Pollatsek, & Bertera, 1982) but morphological information is not (e.g., Kambe, 2004; Inhoff, 1989). These results stand in sharp contrast to the consistent findings reported by Deutsch and her colleagues in Hebrew (Deutsch, Frost, Pollatsek, & Rayner, 2005; Deutsch et al., 2003), suggesting that a parafoveal presentation of a letter string, derived from the same root morpheme as the foveal target word, decreased the processing time of the word when it was later fixated. Interestingly, results from Hebrew-speaking children reveal morphological priming effects as early as grades 1 to 3. These findings are supported by psycholinguistic research showing that children's mistakes at ages 3–5 reflect root extraction (Ravid & Malenky, 2001; Berman, 1993; Clark & Berman, 1987; Berman, 1982), thereby demonstrating that young Hebrew speakers are tuned to root morpheme information before they are explicitly taught the rules and structure of Hebrew morphology. Taken together, studies of adult and beginning readers jointly demonstrate that Hebrew speakers extract morphological information in the process of reading and that this process is early, automatic, and efficient.

Although current opinion is moving more strongly toward some form of morphemic account for lexical architecture, the precise nature of this account remains controversial. Thus, it seems that the theoretical question regarding the role of morphology in processing print may not be resolved by considering behavioral data alone. In recent years, considerable efforts have been made to examine the neural correlates of processing print by producing brain-imaging data. This research consistently identified cortical sites involved in processing orthographic, phonological, and semantic information (Sandak et al., 2004). For example, Pugh and his colleagues suggested that the cortical reading system involves three major components: a posterior ventral circuit including lateral extrastriate areas and a left inferior occipito-temporal area which is related to fast, memory-based orthographic word identification; a posterior dorsal circuit including the angular gyrus and supramarginal gyrus in the inferior parietal lobule and the posterior aspect of the superior temporal gyrus (Wernicke's area), which is involved in relatively slow, rule-based recoding of printed words into phonological representations; and an anterior circuit centered in and around Broca's area in the inferior frontal gyrus (IFG), which is involved in recoding print into the articulatory code that is needed for overt naming (McCandliss, Cohen, & Dehaene, 2003; Pugh et al., 2000). A more refined version of this neurobiological model suggested that the ventral system includes two functionally distinct components. The posterior aspect of the ventral system (OT) is a "visual word-form area" or "skill zone" that transforms visual patterns into codes that are maximally efficient for activating the phonological and semantic information associated with printed words (McCandliss et al., 2003). Anterior aspects of the ventral system (MTG; inferior temporal gyrus [ITG]) were found to be semantically tuned regions which bind semantic features that are widely distributed across the brain. This neurobiological model was heavily influenced by the computational principles embodied by the triangle framework of the PDP framework (Harm & Seidenberg, 1999, 2004; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989) and does not directly address the processing of morphological information in the brain.

Interestingly, there have been but few attempts to examine the neural networks involved in morphological processing, and the results of these studies seem inconclusive. For example, although several studies found that generating irregular verbs demands far more neural resources than regular verbs, they were quite disparate regarding the location of this activation (Davis, Meunier, & Marslen-Wilson, 2004; Tyler, Bright, Fletcher, & Stamatakis, 2004; Beretta et al., 2003); others found a totally opposite pattern with an increase in activity for regular verbs (Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005). Finally, Sach, Seitz, and Indefrey (2004) found no dissociation for verb regularity at all. In a recent study, directly comparing morphological priming with orthographic and semantic priming, Devlin, Jamison, Matthews, and Gonnerman (2004) failed to find any morphologically related activation that could not be explained as the joint result of semantic and orthographic properties.

One possible account for the apparent inconsistencies in finding neural correlates of morphological processing is that many imaging studies were conducted in English, which is characterized by a relatively impoverished morphological structure. This hypothesis, however, requires empirical investigation. The present study is an initial attempt to examine and identify the neural circuitry involved in morphological processing in a morphologically rich language such as Hebrew.

We conducted a functional magnetic resonance imaging (fMRI) experiment in which subjects were engaged in explicit morphological processing where they were required to determine whether two paired words had a common root. Hebrew provides a unique opportunity to isolate the influence of semantic transparency in morphological processing. We, therefore, created two lists of morphologically related words, one that involved semantic overlap, and one in which the root derivations were not semantically related. Subjects were also asked to perform semantic, phonological, and orthographic similarity judgments on other stimuli to allow evaluation of the relation between processing of morphology and processing of other components of language. This experiment was designed to determine the significance of morphological processing and whether it can be distinguished from the joint semantic, orthographic, and phonological activation.

METHODS

Participants

Fourteen healthy volunteers participated in this study (7 men, 7 women, ages ranging from 20 to 50 years, mean age = 28.3 ± 7.2 years, 13 were right-handed). All participants were native Hebrew speakers, without any neurological record or reading disorders. Participants gave written consent before taking part in the study. Ethical approval was granted by the Tel-Aviv Sourasky Medical Center.

Magnetic Resonance Protocol

The blood oxygenation level dependent (BOLD) fMRI measurements were performed in a whole-body 1.5-T Signa Horizon, LX8.25 General Electric scanner. BOLD contrast was obtained with a real-time gradient-echo echo-planar imaging (RTEPI) sequence and a standard head coil. Functional data were obtained using TR =

3 sec, TE = 55 msec, flip angle = 90°, imaging matrix = 64 × 64, FOV = 21 cm and 27 slices, 4 mm each, in the axial direction covering the whole brain. High-resolution (0.82 × 0.82 mm in-plane) T_1-weighted anatomical images were acquired at the same orientation to allow accurate alignment with a three-dimensional spoiled gradient-echo (SPGR) sequence (0.93 × 0.93 × 1.2 mm).

Experimental Setup

All words were visually presented via an LCD projector (Epson MP 7200, Japan) 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 motor response box. Subjects responded with the right index finger for ''yesh answers and the left index finger for ''no'' answers.

Experimental Design

The experiment included five tasks: a semantic task in which the subjects had to decide whether the two words were related in meaning; a morphological task in which they had to decide whether the two words were derived from the same root; a phonological task in which the subjects had to decide whether the two words rhymed; an orthographic task in which subjects decided whether two words looked orthographically similar (i.e., whether they differed in no more then one letter); and finally, a visual control task in which subjects were asked to judge whether two line patterns were identical (e.g., //\\\ ///\\). The morphological task consisted of two different conditions, one in which the morphologically related words were also semantically related (+M+S), and one in which they were not (+M−S); subjects were not notified of the internal structure of the morphological task. The different tasks were presented to the subjects in a block design.

Each block consisted of the following events: (1) A phrase announcing that a new task is about to begin was presented, and was followed by two lines of alphanumeric symbols. The announcement lasted for 6 sec; its aim was to focus the subjects' attention on the upcoming instructions, and the symbols were presented to create a baseline of familiar, unreadable, word-like stimuli. (2) An instruction phrase followed, notifying the subject what type of judgment was required for the following block (e.g., ''press yes if the two words have the same root,'' ''press yes if the two words rhyme,'' etc.). This instruction was presented for 3 sec. (3) Following the instruction, the relevant task block was presented. Task blocks always consisted of five pairs of words; each pair was presented for 1.5 sec and was followed by a 2.1-sec interstimuli break to allow for responses. Altogether the task block lasted 18 sec and the interblock interval lasted 9 sec, including presentation of instructions (see Figure 1). Task blocks were presented in a counterbalanced pseudorandom order, and the order of pairs within the blocks was set randomly. The experiment was divided into two sessions, each lasting 11.1 min; the order of the sessions was balanced between subjects. To ensure subjects' adequate performance during the experimental session, an 11-min training session was administered before entering the magnet. The training session was similar in structure to the actual experiment. Response times and accuracy were recorded.

Stimuli

Two hundred pairs of words were used in this experiment (40 pairs of words for each of the five linguistic conditions; semantic, +M+S, +M−S, phonological, and orthographic). One hundred additional pairs were used

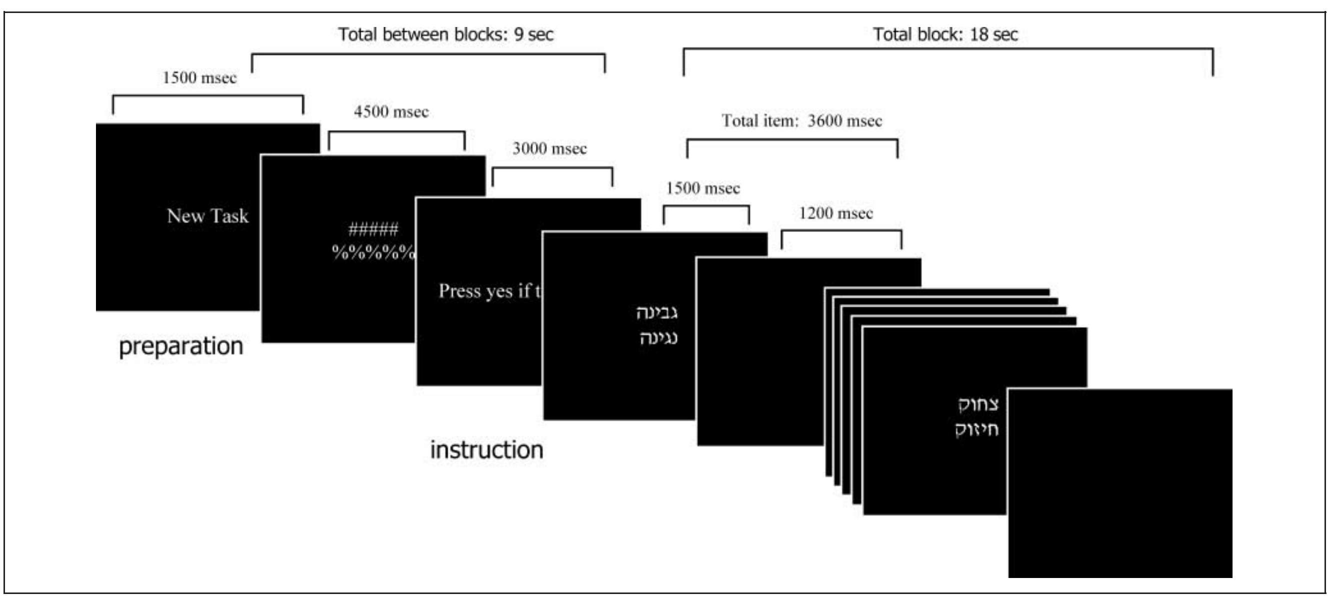

Figure 1. The sequence of events in a single block.

for the training session (for examples of stimuli in the five conditions, see Table 1). All words were common Hebrew nouns. The words used in the semantic and morphological experimental conditions were all derived from productive roots and had a three-letter root (i.e., weak roots were not employed; see Frost, Deutsch, & Forster, 2000). To prevent repetition effects, all words and roots in the experiment appeared only once. Line patterns included five lines directed right or left and were either identical or differed by one line orientation. Because there are only 32 possible combinatorial possibilities, patterns appeared more than once.

Methodological Considerations

The following methodological precautions were taken to ensure that subjects' decisions were based solely on the linguistic properties we wished to examine: (i) To prevent decisions based on orthographic features in the phonological task, the nonrhyming words were chosen to be as orthographically similar as the rhyming words (all words shared the final one or two letters). In addition, we included words that rhymed but had different ending spelling. (ii) To minimize orthographic effects in the morphological task, all nonrelated words were as orthographically similar as the related words (all shared at least 3 letters). (iii) To prevent semantic influences in the morphological task, the morphologically unrelated pairs of words (those used for the "no" responses) in the +M+S blocks were semantically related as well. Considering the constraints of the experiment (whole roots only, finding words that are +O−M+S, etc.), it was impossible to match the semantic relatedness of the stimuli. Our aim, however, was to focus on the cognitive process derived by the task (i.e., the actual judgment of semantic similarity) rather than by the stimuli, so that stimuli were selected to ensure successful performance of the task. All tasks were designed such that half of the pairs were related and half were not. Thus, there was a probability of .5 for a "yes" or a "no" response. Note that even when the words were not related, the task, nevertheless, required concentrating on the desired process (e.g., retrieving the semantic meaning, finding the root morpheme, etc.). Therefore, we did not differentiate between responses to related and nonrelated stimuli.

Data Analysis

Data analysis was performed using the BrainVoyager 4.96 and 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 space (Talairach & Tournoux, 1988), *Z*-normalized, and concatenated.

Changes in BOLD contrast associated with the performance of the reading tasks were assessed on a pixel-by-pixel basis using the general linear model (Friston, Frith, Turner, & Frackowiak, 1995); the hemodynamic response function was modeled using standard parameters (Boynton, Engel, Glover, & Heeger, 1996). Group analyses were investigated using random effect analysis ($p < .002$). In order to correct for errors due to multiple comparisons, effects are reported only for clusters larger than threshold estimator based on Monte Carlo simulation ($p < .05$).

Functional images were superimposed on two-dimensional anatomical images and 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

Table 1. Examples of Stimuli

	Hebrew	*Orthographic Trans.*	*Phonetic Trans.*	*Semantic Meaning*
Semantic	כביש	**kb**y**S**	kvish	Road
	נתיב	**nt**y**b**	nativ	lane
Morphologic	מנהג	m**nhg**	minhag	custom
	נהיגה	**nh**y**g**h	nhiga	driving
Morphologic + Semantic	משפט	m**Spθ**	mishpat	trial
	שופט	**S**w**pθ**	shofet	judge
Phonologic	גבינה	**gb**y**n**h	gvina	cheese
	נגינה	**ng**y**n**h	ngina	playing (music)
Orthographic	מחול	m**xw**l	maxol	dancing
	מחוג	m**xwg**	mahog	Hand (of a clock)

3-D SPGR scan. 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.

For each of the tasks, activation maps were defined by contrasting the task with the visual control task to remove activation resulting from basic visual properties, response selection, and motor response. Further analysis included direct contrasts between the language conditions.

Regions of interest (ROI) for morphological tasks were defined for each subject individually in the following way: For each subject individually, morphologically specific activation ($p < .05$ not corrected) was identified for each of the morphological conditions separately by contrasting each of the morphological tasks with the other language tasks. Activated voxels located within 20 mm of the multisubject activity center were defined as ROI. ROI defined by one morphological condition was used to evaluate the activation during the other morphological condition. For each ROI, the averaged temporal pattern and the bar histograms of the percent signal change for the different tasks were calculated. These bar histograms include the average activation from all subjects during stimuli blocks with time-shift to allow for hemodynamic response (t = 6–18 sec).

RESULTS

Behavioral Results

The mean accuracy and reaction time are shown in Figure 2. Overall, subjects displayed adequate performance in all tasks (average error rate for all tasks was 6.25 ± 1.67), and no block contained more than two errors (indicating misunderstanding the task or missing the instruction). Reaction times to correct trials were entered into a three-way analysis of variance with task, session, and list as independent factors, revealing a main effect of task [$F(1, 10) = 12.188$, $p < .001$], thereby indicating that subjects found the semantic and the morphological tasks in the +M+S condition easier than the other linguistic tasks ($p < .001$). In all linguistic tasks there was a high correlation between error rate and reaction time ($R^2 = .9787$), allowing us to consider them both an accurate measure for task difficulty. In the visual task, reaction time was not correlated with accuracy. This was probably the result of the bird cage head coil that could have masked sometimes a line in the pattern, and thus, caused more errors in this relatively easy task. There was neither a significant main effect of session nor of word list, thus showing that the training was sufficient as subjects' performance did not improve significantly during the experiment. No significant interaction between task and session or word list was found.

Imaging Results

Initial analysis of the imaging data identified the neural circuits engaged in word reading by contrasting activation in all linguistic tasks to activation in the visual line task. This process revealed activation in several areas in the left hemisphere including most of the lateral frontal lobe, the occipito-temporal region, the middle temporal gyrus, and the parietal lobe. All of these areas are known to be involved in processing visually presented words (for a review, see Demonet, Thierry, & Cardebat, 2005; Price, 2000). No significant cluster was found in the right hemisphere.

Activated areas in the different judgment tasks are listed in Table 2 and presented in Figure 3. Each of the judgment tasks activated large regions in the left inferior and middle frontal lobe. The semantic related activation was more anterior and inferior relative to the orthographic and phonological activation and was restricted to a smaller region. In addition, semantic judgment of words resulted in activation in the superior temporal sulcus (STS), consistent with previous word judgment tasks in the visual modality (e.g., Seghier et al., 2004; Pugh et al., 1996). In a more lenient threshold ($p < .005$), the OT was activated by the semantic task in correspondence to finding that OT is automatically activated in word processing. Orthographic

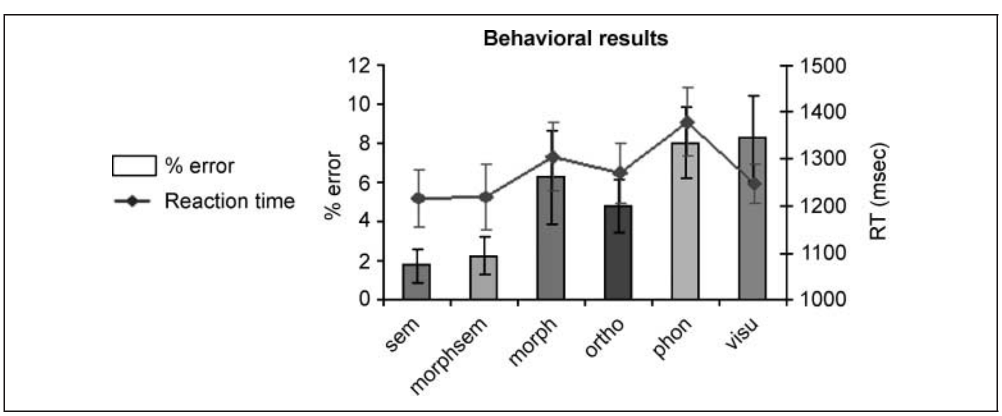

Figure 2. Accuracy and reaction time (RT) results from 10 subjects. Analysis of variance showed no significant influence of session or order of sessions. Both RT and accuracy are significantly influenced by task.

Table 2. Significant Activations during the Tasks as Defined by the Contrast of the Specific Language Task (the Morphological Task Includes Both Conditions) Minus the Visual Control Task

	BA	Mean x	Mean y	Mean z	Z at Peak Voxel	Cluster Size (mm)
(a) Semantic Task						
Left lingual gyrus*	17	−18	−88	−6	8	430
Left middle temporal gyrus, STS	21/22	−49	−36	3	5.2	544
Left middle frontal sulcus, precentral gyrus**	6	−36	5	34	6.1	289
Left middle frontal gyrus*	45/46/47	−44	23	19	10.2	5331
Left medial frontal gyrus*	8	−3	46	42	6.6	458
(b) Morphological Task						
Left lingual gyrus*	18	−17	−86	−6	8	663
Left occipito-temporal sulcus, fusiform gyrus*	19/37	−38	−61	−12	7.1	1280
Intraparietal sulcus, angular gyrus**	39	−32	−61	34	5.5	927
Right cuneus	18	8	−72	20	7	291
Left superior temporal sulcus, middle temporal gyrus**	21/22	−50	−33	1	6.1	1102
Precentral gyrus	6	−42	0	50	5.8	300
Left middle, inferior frontal*	45, 46, 9	−42	19	24	11.8	9607
Caudate nucleus**		−15	8	3	6.4	532
(c) Orthographic Task						
Left lingual gyrus*	18	−17	−86	−6	8.3	643
Left fusiform gyrus, occipito-temporal sulcus*	19/37	−40	−59	−12	6.9	2582
Right cuneus**	18	4	−71	19	6.2	244
Left interparietal, precuneus**	39/19	−31	−66	37	5.9	717
Left middle temporal gyrus*	21	−50	−30	0	6.1	616
Bilateral cingulate gyrus*	31	−0	−31	30	8.7	885
Thalamus		−3	−13	12	6.3	345
Left inferior, middle frontal*	44, 45, 46, 9	−43	21	24	11.5	10825
(d) Phonological Task						
Left lingual gyrus*	18	−18	−87	−7	7.5	303
Left interparietal, precuneus gyrus**	39	−32	−65	36	5.6	559
Occipito-temporal, fusiform gyrus*	19/37	−43	−52	−12	6.2	1321
Left medial calcarine sulcus**	19	−23	−30	0	6.2	351
Left precentral gyrus**	6	−46	−5	48	5.8	662
Left inferior middle frontal*	45, 46, 9	−42	18	24	10.4	10,032

*Voxels in cluster are significant at $p < .0005$.

**Voxels in cluster are significant at $p < .001$.

judgment also activated the STS as well as the interparietal sulcus (IPS). Furthermore, it activated several regions in the occipito-temporal region (OT), including the area known as the ''visual word-form area'' (VWFA). This is consistent with the view that this area is involved in processing word form (Cohen et al., 2000, 2002; Fiebach,

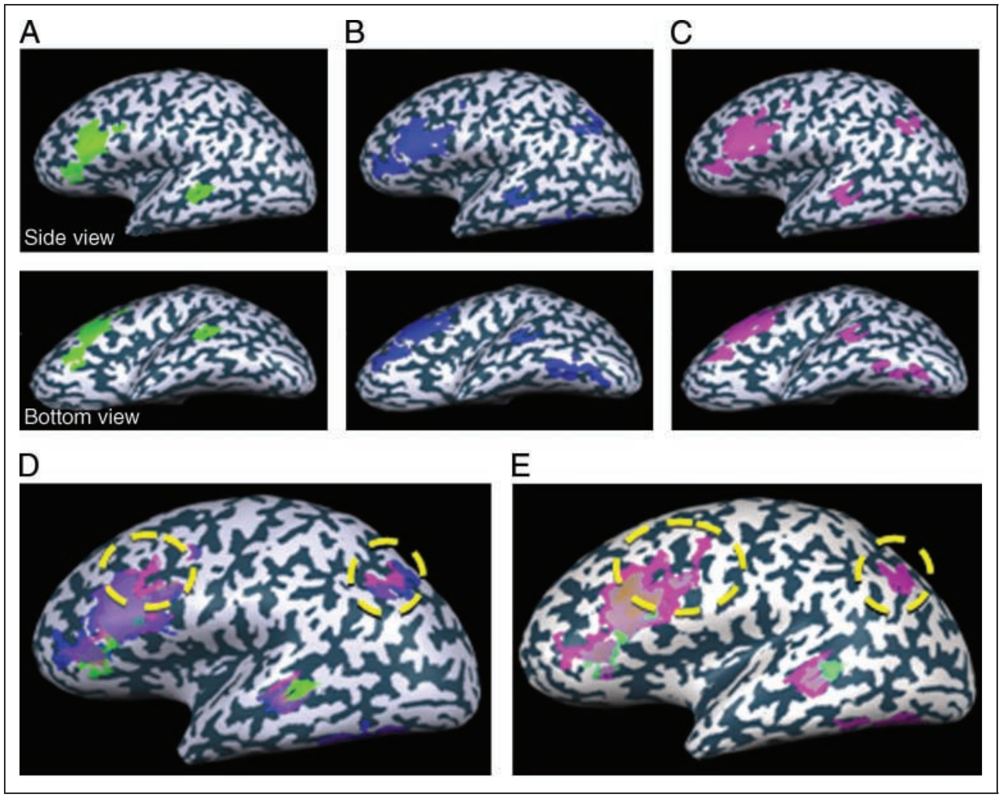

Figure 3. Statistical parametric map of 14 subjects using random effect GLM analysis ($p < .002$, cluster size corrected) during the different tasks contrasted with the visual control task. Maps are presented on an inflated brain of one subject, presented from the lateral (above) and ventral (bellow) view. (A) Semantic activation map. (B) Orthographic activation map. (C) Morphologic activation task (including both morphological conditions). (D) The three maps overlaid (semantic = green; orthographic = blue; morphologic = pink). Comparing morphologically related activation to semantic and orthographically related activation, it is clear that although partial overlap exists, there are clear loci of distinct morphologically related activation (marked in yellow). (E) the semantic condition (light green) and the +M+S condition (pink). Although the maps partially overlap (marked in gray–purple), there are large regions in the left IPS and in the posterior parts of the left MFG (marked in yellow) that were activated by the morphological task and not by the behaviorally matched semantic task.

Friederici, Muller, & von Cramon, 2002). In addition, phonological judgment activated the frontal lobe, regions in the IPS, and the OT. Generally, activation maps coincide with previous imaging studies of semantic, phonological, and orthographic processing of visually presented words (e.g., Sandak et al., 2004; Seghier et al., 2004).

We now come to the analysis of the morphological task, which was the main focus of the present study. The morphological task (the +M+S and +M−S conditions put together) activated the middle and inferior frontal gyrus, the IPS, the supramarginal gyrus, the STS, and regions in the occipital–temporal gyrus, around the VWFA.

In order to compare location of activation during morphological tasks to activity related to other linguistic tasks, we overlaid the activation maps of the different tasks. We found that the locations of the morphologically related activation neighbored locations of semantic and orthographic related activation, but only partially overlapped, as shown in Figure 3D (for a comparison of the +M+S condition and difficulty matched +S condition, see Figure 3E). Loci of morphologically related activation that did not fully overlap with semantic or orthographic related activation were found in the left middle frontal gyrus (MFG) and in the left parietal lobe.

To further differentiate morphological processes from the other linguistic processes, we searched for areas activated by the morphological task to a higher extent than in the other language tasks. Contrasting both morphological conditions with all of the other language conditions (semantic, orthographic, and phonological tasks), we identified two loci of activation (random effect, $p < .001$) around the left IPS and around the left MFG (see Table 3). These findings correspond to the locations identified by the activation maps. Activation in these areas was significant (random effect, $p < .001$) also when the morphological conditions were contrasted directly with the semantic condition. To assess the specific contribution of each of the conditions to the contrast, pairwise t tests were conducted between the activation levels (as measured by percent signal change) in each of the morphological conditions and in each of the other language-related tasks. In both the left MFG and

Table 3. Significant Activations for the Contrast of Morphological Task Minus the Other Three Language Tasks

	BA	*Mean x*	*Mean y*	*Mean z*	*Z at Peak Voxel*	*Cluster Size (mm)*
Left middle frontal gyrus*	46/9	−43	19	30	5.2	271
Left interparietal sulcus, angular gyrus**	39	−33	−59	34	5.7	454
Right lingual gyrus	18	9	−81	−9	5.9	137

*Voxels in cluster are significant at $p < .001$.

**Voxels in cluster are significant at $p < .0005$.

the left IPS, activity in each of the morphological conditions was significantly higher than in any of the other conditions (Figure 4). Moreover, no significant difference between the two morphological conditions, +M+S and +M−S, was found.

To further validate our results, ROIs were defined for each subject individually in the MFG and IPS (see Methods). An across-subjects paired t test in ROIs defined by the +M+S task revealed higher activation in the +M−S condition compared with the semantic condition alone (MFG, $p < .006$; IPS, $p < .0065$), the orthographic condition (MFG, $p < .0015$; IPS, $p < .006$), and the phonological condition (MFG, $p < .0012$; IPS, $p < .01$). Similar results were obtained for +M+S condition using the ROIs defined by the +M−S condition (see supplementary data).

To understand the network involved in morphological processing and its relationship to the areas involved in reading regardless of the task, we proceeded to analyze the activation in areas that were involved in the +M+S condition relative to the visual control task (this condition was chosen because it resulted in the most robust activation). Activation histograms from four regions that were activated for all subjects are presented in Figure 5. All regions seemed to be activated specifically by language—that is, for all language-related conditions, activation was significantly higher than in the visual control task. In the left IPS, activations in both morphological conditions were higher than in any of the other language conditions. In the frontal lobe, the morphological related activations were significantly higher than in the phonological and orthographic conditions, but failed to

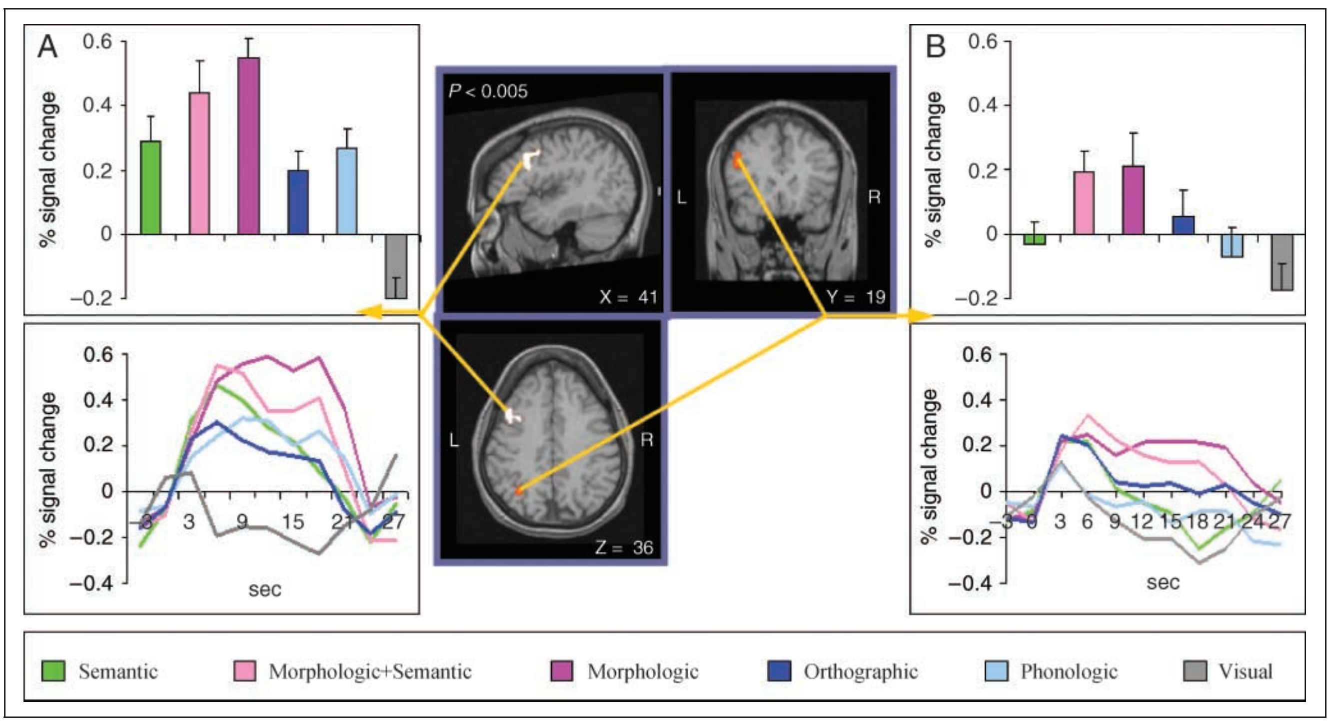

Figure 4. ROIs were selected from multisubject maps using random effect GLM analysis ($p < .005$, corrected for cluster size) contrasting both morphological tasks to all other language tasks (semantic, phonologic, and orthographic). For each ROI, averaged hemodynamic response curves and bar histograms of the percent signal change for the different tasks (morphological task = pink; semantic task = green; orthographic task = blue; phonological task = pale blue; and visual task = gray) were calculated. Bar histograms include average activation for all subjects during stimuli block with shift to allow hemodynamic response (t = 6–18 sec). Averaged hemodynamic response curves and bar histograms are presented for the left MFG (A) and the left IPS (B). A within-subjects pairwise t-test analysis revealed that, in both ROIs, activation in each of the morphological tasks was significantly greater than activation in any of the other tasks. No significant difference was found between morphological tasks, thereby eliminating the possibility of significant semantic influence.

reach a significant difference from the semantic condition. This probably results from our choice of the ROI: The frontal ROI spread out beyond the region identified above as being involved in morphological processing and included more anterior parts of the MFG and the IFG, regions known to be involved in lexical–semantics.

The other areas activated by the morphological condition show a mixed pattern. Activations in the OT during form-related tasks (morphology, phonology, and orthography) were higher than during the semantic task, but this difference reached significance only for the orthographic task ($p < .04$) and in the +M+S condition ($p < .02$). No significant difference was found between activation in the morphological tasks and in the orthographic or the phonological task. An opposite pattern was displayed in the STS: Activations during both morphological conditions were similar to activation during the semantic task, and in all three conditions activations were significantly larger than those obtained during the orthographic or phonological tasks. The lingual gyrus was also significantly activated during the morphological task but the only significant difference between the language conditions in the lingual gyrus was between the +M+S condition and the semantic condition. Interestingly, although the regions were defined by the +M+S condition, the difference between the two morphological conditions was not significant in any of the regions.

Task Difficulty

Note that although there were significant differences between the difficulties of the different tasks, these differences were not reflected in the activity in the regions we identified as morphologically related. On the contrary, although the behavioral results for the +M+S condition were similar to those of the semantic task, the pattern of activity in these regions (as measured by percent signal change in ROIs) in response to this task resembles the response to the +M−S condition and differs significantly from the response to the semantic task. The same pattern exists between the +M−S condition and the phonological and orthographic conditions: Although the behavioral results are similar, in

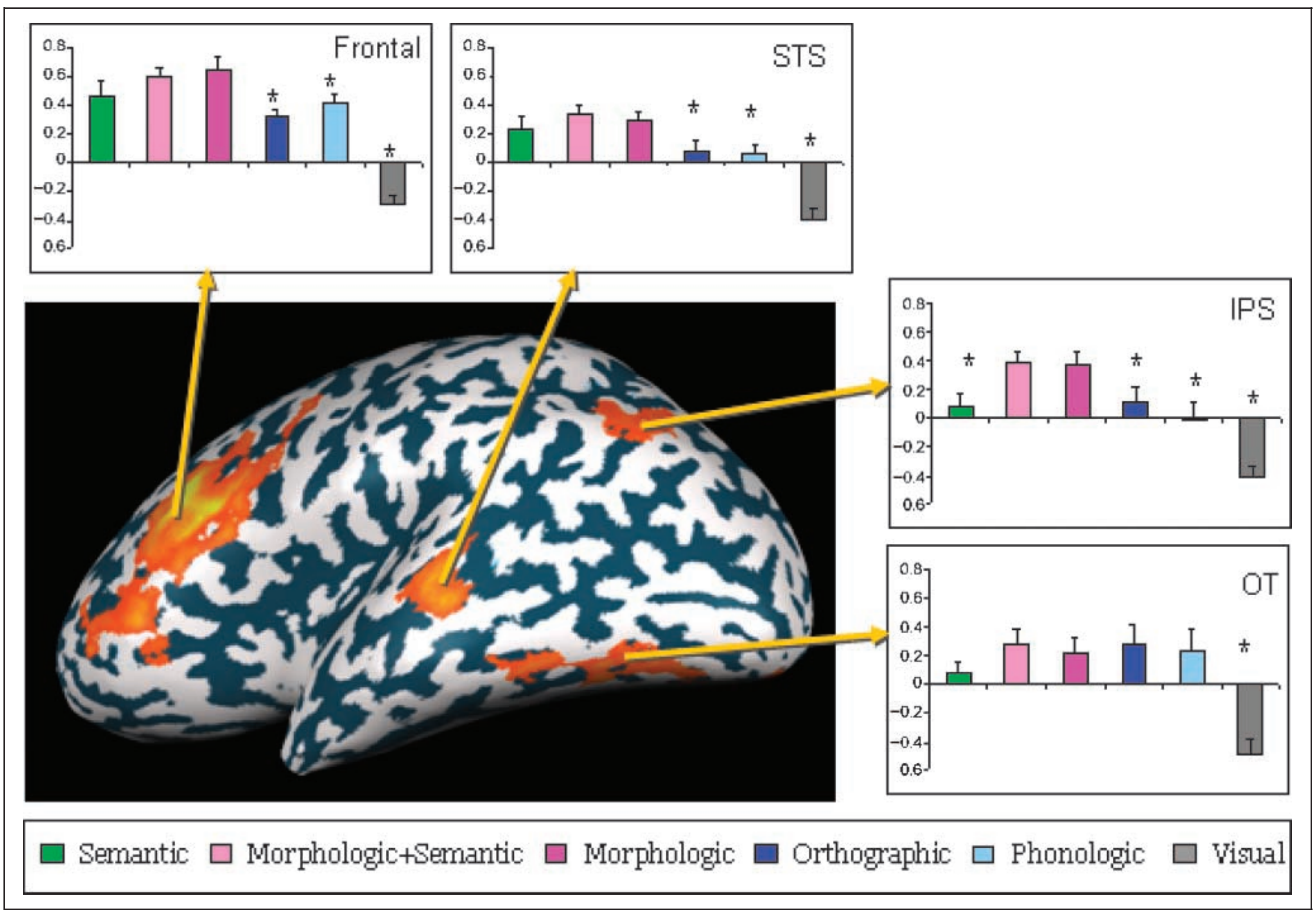

Figure 5. Activation in areas detected by contrasting the morphologically and semantically related condition to the visual conditions ($p < .002$, cluster size corrected. Activation in lingual gyrus is not shown). Bar histograms of the percent signal change are presented (calculated as described above). In the IPS and, to a smaller extent, in the frontal lobe, the activations during both morphological conditions were higher than during the other language tasks. The STS is activated by the morphological conditions as well as by the semantic condition, and the OT during the form-related tasks (orthography, phonology, and morphology) is activated higher than during the semantic task.

the morphologically related regions the response to the tasks in entirely different. These results clearly show that responses are task dependent rather than difficulty dependent.

DISCUSSION

The aim of the present study was to examine whether morphological processing, during Hebrew reading, can be identified as a distinct linguistic component that is not reflected simply by the fine tuning of semantic, phonological, or orthographic structure. Therefore, we investigated whether spatial–temporal clusters that are related exclusively to morphological activity can be identified. Our results seem straightforward: We identified in the left hemisphere exclusive areas that are involved in morphological processing—the posterior MFG and the IPS. The independence of morphological processing in these areas was established both by comparing activation maps of the different tasks and by comparing percent signal changes in the ROIs of the different tasks. Not only could we identify areas where morphological related activation did not overlap with activation related to the other linguistic processes but we also found that, in these areas, activation during each of the morphological conditions, individually, was significantly higher than during any of the other language tasks.

Although the effects in the left IPS were pronounced, in the frontal lobe the differentiation between the +M+S condition and the +S condition was less significant. This might be a result of the intensive involvement of the frontal lobe during semantic processing. Furthermore, the use of real words automatically activated morphological and semantic processing during both conditions, causing additional difficulty in separating the two effects. Additional research is necessary to determine the exact relationship between morphological and semantic activity in the frontal lobe. As the main aim of this article was to prove the existence of distinct morphologically related activity, the evidence from the IPS alone is sufficient.

The results from Hebrew provide the first substantial evidence for the independence of morphological processing. Previous studies in Indo-European languages have identified regions involved in grammatical processing such as gender judgment (e.g., Longoni, Grande, Hendrich, Kastrau, & Huber, 2005; Miceli et al., 2002) or processing regular and irregular verbs (e.g., Tyler et al., 2005; Beretta et al., 2003). However, these studies did not directly address morphological processing per se, and, therefore, the activation recognized in these studies could not be related exclusively to the processing of morphological structures. Furthermore, their methodology did not enable a clear disassociation of the morphological factors from the semantic and orthographic factors.

The Influence of the Semantics on Morphological Judgment

To examine the independence of morphological and semantic processing, we employed two types of morphologically related stimuli: in one, the stimuli were semantically related, and in the other, they were not. This unique property of the Hebrew language allowed us to separate effects deriving from the perception of morphological relatedness from those related to the perception of simple semantic overlap. Note that, in both cases, the task was identical—to decide whether the two words were derived from the same root. The behavioral results show that when words were semantically related, the task was somewhat easier. This finding is in line with previous behavioral data showing stronger priming effects for +M+S word-pairs than for +M−S word-pairs (Frost, Deutsch, Gilboa, et al., 2000). However, in contrast to the behavioral findings, the activation data did not reveal significant differences in the processing of +M+S and +M−S words in those areas that we identified as morphologically related. This finding suggests that morphologically related activity does not result from the semantic relations between the words, nor does it depend on it.

Regions Activated during Morphological Processing

In addition to the areas we identified as being uniquely involved in morphological processing, a wide network of areas was activated during the morphological task. The overlap between those areas implicated by the morphological tasks and areas involved in other linguistic tasks reflects high-level processes that are necessary for reading, comparing words, and making decisions regarding them. Because in the present experiment all conditions (except the line judgment task) included real words (having an orthographic form, a phonological structure, and a semantic meaning), all conditions may have activated all of the areas related to reading to some extent. Although using nonwords might have minimized this overlap, we chose not to do so because the language processing of nonwords is essentially different than the processing of words. Furthermore, in the case of the phonological task, it is impossible to ensure an unequivocal reading for the nonwords (due to the missing vowel information in printed Hebrew).

Analysis of the activation in the areas activated by the +M+S condition reveals some of the relations between the activations produced by the different tasks. The STS was activated by both the morphological task and the semantic task. Importantly, although activation in the +M+S condition was higher than in the +M−S condition, this difference was quite small and not significant, indicating that the semantic similarity between the words had little effect on this activation. This area is known to be engaged in semantic processing, regardless of the input modality (Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). As a result, the activation during the morphological task might be related to the lexical–semantic properties often associated with morphology rather than to morphology per se (as found by Devlin et al., 2004). An alternative explanation could be that this semantic activation during morphological processing is not related to the morphological task but rather to semantic processing. For orthographic and phonological judgment, a shallow processing level is sufficient and the STS is not recruited, whereas morphological judgment requires further processing of the word so additional semantic processing is necessary and the STS is automatically activated.

The OT area was activated by the morphological task, as well as by the orthographic and phonological task. In this area, morphologically related activation was not significantly different than in the orthographic and phonological tasks, and semantic judgment activated this area to a lesser extent. Similar findings were reported by Devlin et al. (2004). A possible explanation for this pattern of activity is that activation in the OT area is not exclusively related to morphological processing, but rather to word-form processing common to both morphology and orthography (Cohen et al., 2000, 2002; Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002; Dehaene et al., 2001). This still does not rule out the option that the OT has a significant part in processing morphological properties of words. The similar activation might be due to the early role of this area in visual word decomposition, which is automatic (Wheatley, Weisberg, Beauchamp, & Martin, 2005) and it might, therefore, be activated by reading, regardless of the task. Adaptation methods such as priming would be necessary to determine whether this area is related to morphological decomposition.

Although the semantic condition activated the OT ($p < .005$), it was to a lesser extent than the other linguistic conditions ($p < .002$). However, because the semantic task induced strong activation in other brain areas related to semantic processing (e.g., left MTG), we do not consider this outcome to reflect on the general strength of the semantic condition. This pattern of activation in the OT may be a result of its strong involvement in word-form processing (Devlin, Jamison, Gonnerman, & Matthews, 2006; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Pugh et al., 2000). Hence, the tasks involving form analysis may have induced an increase in activation beyond the activation needed in processing words in general.

The Region Specifically Involved in Morphological Processing

Both the left MFG and the left IPS are known to be involved in reading (e.g., Seghier et al., 2004) and, specifically, were found to show differential activation to verbs and nouns (Shapiro, Moo, & Caramazza, 2006) and in grammar-related tasks (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Tyler et al., 2005). A recent study has shown both these areas to be active in a morphological derivation task as well (Marangolo, Piras, Galati, & Burani, 2006). In this study, Marangolo et al. found that the areas we identified as being involved in morphological processing were activated in the process of generating derivations of Italian words, as well as inflections of verbs, but not of adjectives or nouns. These areas were also activated differentially for derivations and inflections of verbs. The correspondence to our results suggests that the involvement of the left MFG and the left IPS in morphological processing is not task dependent.

Posterior regions in the parietal lobe are known to be active in lexical semantics (Alexander, Hiltbrunner, & Fischer, 1989). More specifically, these areas were found to be sensitive to sentence complexity (Constable et al., 2004) and to be involved in complex interactions between semantics and phonology (Frost, Mencl, et al., 2005). In addition, this area displayed a decrease in activation as a result of morphological priming (Devlin et al., 2004), although this decrease was not stronger than that caused by semantic or orthographic priming.

Several studies found activity related to morphology in the left IFG and the left MFG regions. Stronger activation in the left IFG was found for inflected Finnish words compared with morphologically simple words (Lehtonen, Vorobyev, Hugdahl, Tuokkola, & Laine, 2006; Laine, Rinne, Krause, Teras, & Sipila, 1999). This area was differentially activated for regular versus irregular verbs, but the direction of the effect has been inconsistent (Tyler et al., 2005; Beretta et al., 2003). Furthermore, studies of grammatical gender representation reveal that when morphology is used to retrieve gender information, the superior and posterior portion of BA 44 is activated, as well as BA 45/47, whereas when morphology does not aid grammatical gender judgment, the activation is focused in the inferior tip of BA 44 (Heim, Alter, & Friederici, 2005; Longoni et al., 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.

The loci of these frontal activations are congruent with the area in the frontal lobe that we identified as related to morphological processing, although the locations presented in some of the studies are somewhat inferior and anterior relative to our results (e.g., Heim et al., 2005; Tyler et al., 2005). In our experiment, significant morphologically related activation did extend to the more anterior and inferior frontal lobe, but because this area was activated in the other tasks as well, we could not safely define these areas as exclusively related to morphological processing. Because these experiments did not directly address morphological decomposition, issues such as word length (morphologically complex words are longer than simple words), semantic and orthographic relatedness, grammatical regularity, and rule versus memory can explain the differences in the exact locus of activation. Furthermore, most of these studies used morphological inflections; the processes involved in derivation analysis might be of a different nature (Marangolo et al., 2006).

Our results differ significantly from previous results reported by Devlin et al. (2004), who failed to find distinct morphologically related activation in English word processing. Our experiment differed from theirs in both language and paradigm: Devlin et al. used an implicit priming paradigm, whereas our experiment required explicit morphological processing. Devlin et al. suggested that a different pattern of results might be found in languages with a richer morphology, such as Hebrew. Behavioral studies, indeed, show a different pattern of activation for Semitic and Indo-European languages, which may very well be reflected in brain activity. Davis et al. (2004) suggested that the reason that they failed to find differences in activation between morphologically simple and complex words is that although explicit morphological tasks can invoke overt morphological activation, on-line language comprehension might not activate these areas. Additional studies using the same paradigm in both languages are necessary in order to determine the cause for this inconsistency.

Our findings regarding morphological processing are consistent with Dominguez, de Vega, and Barber (2004), who found a systematic contrast between ERPs of morphological priming and other sources of possible confounding: stem homographic, orthographic, and synonym priming. They concluded that the modulation of the N400 by morphological priming cannot be explained by the connectionist models but rather indicate that morphological processing is a distinct linguistic process. Similar results were found by Stockall and Marantz (2006) using magnetoencephalography. These results from imaging methods that are sensitive to the temporal aspect of processing support our conclusions regarding morphological processing.

In conclusion, the present study provides evidence concerning the existence of morphologically related activity in an explicit task design. We identified two locations involved in morphological decomposition of visually presented words, one in the left MFG and the other in the left IPS. Furthermore, we showed that this activity does not result from the joint contribution of orthographic and semantic properties. Because our results show activation that is independent of the semantic overlap between words, the possibility that this activation results from semantic factors alone seems unlikely. These results coincide with the behavioral data previously obtained in Hebrew, demonstrating the important role of morphological processing in reading, thereby suggesting that morphological analysis is a significant process in visual word recognition, distinct from other processes.

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