Neural Correlates of Morphological Decomposition during Visual Word Recognition

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Abstract

■ Considerable behavioral research has demonstrated that the visual word recognition system is sensitive to morphological structure. It has typically been assumed that analysis of morphologically complex words occurs only when the meaning of these words can be derived from the meanings of their constituents (e.g., hunter = hunt + er). However, results from recent behavioral research using the masked priming technique have demonstrated that morphological analysis can occur at an earlier orthographic level, in cases in which the meanings of complex words cannot be derived from their constituents (e.g., corner = corn + er). Here, we combine the logic of behavioral masked priming with the neurophysiological phenomenon of functional magnetic resonance imaging priming suppression to look for evidence of nonsemantic morphological priming at the neural level. Both behavioral and functional magnetic resonance imaging results indicated priming effects associated with the mere appearance of morphological structure (corner–CORN). In addition, these effects were distinguishable from lexical–semantic effects (bucket–PAIL) and orthographic effects (brothel–BROTH). Three left-lateralized occipito-temporal regions showed sensitivity to early morphological components of visual word recognition. Two of these regions also showed orthographic priming (∼BA 37, peak: −48 −60 −17; ∼BA 19, peak: −40 −77 −1), whereas one was sensitive only to morphological similarity between primes and targets (∼BA 19, peak: −37 −67 −7). These findings provide a neurobiological basis for a purely structural morphemic segmentation mechanism operating at early stages of visual word recognition. ■

INTRODUCTION

Two well-established components of visual word recognition involve visual form (orthographic) and meaning-based (semantic) processes. The orthographic component involves sensitivity to visual features of letter strings such as sequential dependencies (Olson, Wise, Conners, & Rack, 1990). The semantic component involves sensitivity to the meanings of letter strings that have a lexical status (Strain, Patterson, & Seidenberg, 1995). In addition to having a visual form and an associated meaning, some words have an internal structure, or morphology. Morphology is a subfield of grammar. Morphologically complex words are those that can be decomposed into simple meaningful subunits called morphemes. Morphemes consist of words or meaningful parts of words (e.g., affixes) that cannot be broken down further into smaller meaningful parts. For example, the word "cleaner" can be segmented into the stem "clean" and the suffix –er, providing an agentive function (a person who cleans). There is now considerable agreement that morphologically complex words are somehow decomposed in visual word recognition and analyzed in terms of their constituent morphemes (see, e.g., Frost, Grainger, & Rastle, 2005).

The dominant view of morphological processing in visual word recognition asserts that it is a high-level phenomenon constrained by semantic knowledge (Giraudo & Grainger, 2000; Plaut & Gonnerman, 2000; Rueckl & Raveh, 1999). Both localist and distributed-connectionist expressions of this perspective are based on the notion that morphological relationships provide an important element of structure to the largely arbitrary orthography-to-semantics mapping. These theories posit that in learning the orthography–semantics mapping, letter strings that consistently share orthography and meaning (such as morphological relatives, e.g., "unclean," "cleaner," "cleanliness," "cleanness") will become represented in terms of their constituents (see Rastle, Davis, Marslen-Wilson, & Tyler, 2000, for discussion). Morphological decomposition is therefore proposed to occur only in cases in which morphologically complex words are semantically transparent (i.e., in cases in which their meanings can be derived from the meanings of their constituents; e.g., a "hunter" is someone who hunts). Decomposition is *not* expected in pseudomorphological constructions in which the relationship between the full form and the stem is semantically opaque (e.g., a "corner" is not someone who corns). These theories have been supported by substantial research demonstrating that morphological priming effects are obtained only when primes and targets have a semantic relationship (e.g., Meunier & Longtin, 2007; Rastle et al., 2000; Marslen-Wilson, Tyler, Waksler, & Older, 1994). This support has been restricted, however,

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to paradigms thought to reflect lexical–semantic levels of the language system such as cross-modal priming and visual priming with fully visible primes.

Very Early Morphological Decomposition

Recent results using the masked priming technique have suggested a different view, however. In a typical masked priming experiment, a briefly presented (<50 msec) lowercase prime is sandwiched between a forward mask (e.g., ######) and an uppercase target that acts as a backward mask (Forster & Davis, 1984). Several behavioral studies and, more recently, ERP studies using this paradigm have reported robust priming for pseudomorphological pairs (e.g., corner–CORN) and illegal novel morphological pairs (e.g., spendical–SPEND) that is equivalent in magnitude to the priming observed for semantically transparent morphological pairs (e.g., hunter–HUNT). Critically, these priming effects cannot be ascribed to simple orthographic similarity because they are not observed for prime–target pairs that have a nonmorphological form relationship (e.g., brothel–BROTH; –el never functions as a suffix in English; Lavric, Clapp, & Rastle, 2007; Longtin & Meunier, 2005; Rastle, Davis, & New, 2004; Longtin, Segui, & Hallé, 2003; Rastle & Davis, 2003). These findings have challenged the dominant view of morphological decomposition because they illustrate that morphological priming is not necessarily dependent upon semantic transparency. Instead, results from these masked priming studies have suggested the existence of a mechanism within the visual word recognition system that operates at an early sublexical orthographic level, serving to decompose any letter string that appears morphologically complex (Longtin & Meunier, 2005; Rastle et al., 2000, 2004; Longtin et al., 2003). However, little is known about the neural bases of this early form of morphological segmentation.

fMRI Priming Suppression

In the present study, we combine the logic of behavioral masked priming with the neurophysiological phenomenon of functional magnetic resonance imaging (fMRI) suppression to look for evidence of pseudomorphological priming at the neural level. Several fMRI experiments have reported reduced blood oxygen level-dependent response (fMRI suppression) during trials involving repeated compared to novel stimuli (reviewed in Wiggs & Martin, 1998). Importantly, Dehaene et al. (2001) showed that the phenomenon of fMRI suppression also accompanies short-term priming effects in which the target is preceded immediately by the identical word (identity priming), even under masked conditions in which subjects were unaware of primes. Despite the short duration of primes (29 msec) and the relatively small behavioral priming effect size (~16 msec), robust fMRI suppression was observed in extrastriate and fusiform

cortices of the left hemisphere. Although these identity priming effects likely reflected shared contributions of several different linguistic processes, the study raised the possibility that the neural correlates of these different processes could be fractionated through fMRI suppression studies that vary the kind of linguistic relationship between prime and target.

Only one masked fMRI priming study has explored morphological decomposition during visual word recognition. Devlin, Jamison, Matthews, and Gonnerman (2004) compared fMRI suppression when targets were preceded by primes sharing a relationship that was semantically transparent morphological (hunter–HUNT), orthographic (craven–CRAVE), or semantic (imitate–COPY). Neural morphological priming effects entirely overlapped orthographic effects (in the posterior occipito-temporal cortex) and semantic effects (in the lateral middle temporal cortex). Devlin et al. (2004) argued that these results supported a version of the dominant theory of morphological processing, namely, that morphological effects reflect a convergence of orthographic and semantic similarity. However, the orthographic condition in Devlin et al. consisted largely of pseudomorphological pairs (e.g., corner–CORN). This study did not separate orthographic (e.g., brothel–BROTH) and pseudomorphological pairs into different conditions (as suggested by Davis, 2004), making its results equally consistent with the notion of an early morphemic segmentation procedure that operates independently of semantics.

Thus, despite mounting evidence in support of a form of early morphological decomposition that is independent of lexical–semantic processes, little is known about the neural correlates of this segmentation mechanism. The extent to which this early form of morphological decomposition overlaps lexical–semantic and/or orthographic priming at the neural level also remains unknown. Here, we address these questions using a masked priming study in conjunction with fMRI, employing conditions consisting of pairs sharing a pseudomorphological relationship (corner–CORN), pairs sharing a pure orthographic relationship (brothel–BROTH), and pairs sharing a lexical–semantic relationship (bucket–PAIL). We looked for functional neuroanatomical evidence of morphological, orthographic, and lexical–semantic components of visual word recognition by searching for priming effects within regions that were activated during lexical decision. Figure 1 presents a schematic of the present design.

METHODS

Stimuli

Stimuli included 48 prime–target pairs in each of four word target conditions. Prime–target pairs were selected from the CELEX English database (Baayen, Piepenbrock, & van Run, 1993). Many of the morphological and orthographic pairs were used in Rastle et al. (2004). Pairs in the pseudomorphological condition were semantically opaque, sharing an apparent morphological relationship
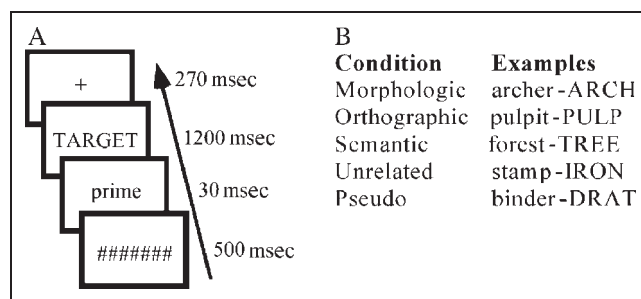
Figure 1. Schematic of the masked priming paradigm and examples of stimuli. (A) Lowercase primes were forward masked by hashmarks and backward masked by uppercase targets. Targets were followed by a fixation cross, warning subjects of the next trial. (B) Targets were either related to primes by morphology, orthography, lexical–semantics, were unrelated, or were pseudowords.

but no semantic relationship (corner–CORN). Pseudo-morphological primes were constructed such that they could be parsed perfectly into the target ("corn") and an English suffix (–er). Suffixes in the morphological condition had an average type frequency of 725 occurrences in English. Pairs in the orthographic condition shared visual form but not morphology or meaning (brothel–BROTH). Orthographic pairs were composed of the target (e.g., "broth") and a nonmorphological ending (e.g., –el) or, in rare cases, a suffix occurring only very infrequently in English (i.e., in no more than three orthographically transparent wordforms; e.g., –st as in "against").

Pairs in the different conditions were very well matched on a number of psycholinguistic characteristics (see Table 1 for mean values of these characteristics across each condition). Pairs in the lexical–semantic condition shared meaning but not visual form or morphology (saloon–BAR). We refer to this condition as lexical–semantic because some pairs were related associatively in addition to semantically (forest–TREE). Pairs in the unrelated condition did not share morphology, visual form, or meaning (distinct–CHEAP). None of the pairs in the lexical–semantic or unrelated conditions began with the same letter, and these pairs shared significantly fewer letters than pairs in the morphological and orthographic conditions.

A total of 96 word–pseudoword trials were included to provide the NO response for the lexical decision task.

Pseudoword targets were constructed by changing one letter of a group of word stimuli not used in the present experiment and were matched with word targets for length. Word primes for pseudowords were matched for frequency and length with primes used in the four word conditions.

Pilot Study

A pilot study was conducted to determine whether presentation of masked prime stimuli for 30 msec could be consciously perceived by participants. Twelve healthy volunteers participated (8 women, mean age = 22.6, $SD = 3.4$). Target stimuli consisted of 40 words and 40 pseudowords selected randomly from stimuli used in the subsequent fMRI study (stimuli described above). Trial structure was similar to that used in the subsequent fMRI experiment. However, in the pilot study, the task involved lexical decisions on the masked lowercase letter strings to determine whether these strings could be consciously perceived. Trials consisted of a 500-msec forward mask (#########), a word or pseudoword presented in lowercase for 30 msec (e.g., corner, floop), and a backward mask consisting of a word presented in uppercase for 500 msec (e.g., TABLE). Word and pseudoword targets were presented in random order. Participants were informed that lowercase letter strings would be presented very rapidly in between a set of hashmarks and an uppercase word. Participants were asked to decide whether each lowercase string was a real English word via button presses. Results indicated that performance was not different from chance, with a mean accuracy of 48.4% ($p = .97$). These results demonstrate that lowercase strings could not be consciously perceived in the present design, even when attention was directed to those strings.

fMRI Study

Participants

Eighteen volunteers who were not involved in the pilot study participated in the fMRI study. Two participants' fMRI data were not analyzed due to within-run movement

Table 1. Mean Values of Primes and Targets in Each Condition

	Orthographic	Morphological	Lexical–Semantic	Unrelated	ANOVA
Target length	4.79	4.79	5.00	4.81	$F(3, 188) = 0.80$, ns
Target frequency	17,731	16,978	18,676	14,848	$F(3, 188) = 0.17$, ns
Target N	3.06	3.02	3.06	3.27	$F(3, 188) = 0.21$, ns
Prime frequency	8393	9314	9869	7900	$F(3, 188) = 0.08$, ns
Shared letters	4.79	4.79	1.10	0.16	$F(3, 188) = 4.4$, $p < .01$

N = orthographic neighborhood; Frequency is per 100 million observations (Burgess & Livesay, 1998); all direct t-test comparisons between conditions were $p ≥ .34$ for variables other than shared letters.

that exceeded 2 mm in one or more directions. The reported results reflect data from the remaining 16 participants (9 women, mean age = 23.6, SD = 4.1). None of these participants moved more than 1.2 mm in any direction. All participants were right-handed, native English speakers, who reported no neurological disease and had normal or corrected-to-normal visual acuity. Participants provided written informed consent in a manner approved by the University of Kentucky Institutional Review Board and were paid for participating.

Task Procedures

Participants decided if visually presented letter strings were words or nonwords. A masked priming paradigm was used similar to that developed by Forster and Davis (1984). Trials consisted of a sequence of four different events. Each event followed immediately the preceding event: a 500-msec forward mask (#########), a prime in lowercase for 30 msec, a target in uppercase for 1200 msec, and a fixation cross for 270 msec (see Figure 1). The lowercase primes were forward masked by the hashmarks and backward masked by the uppercase targets. Participants were told that a series of hash marks would precede targets but no mention was made about primes. Different trial types were presented in pseudorandom order, with a fixation cross presented during a variable intertrial interval to enable fMRI jittering (see below).

Stimulus presentation and recording of responses were implemented with E-Prime software (Psychology Software Tools, Pittsburgh, PA) using an MRI-compatible projection system (SilentVision SV-6011 LCD; Avotec, Stuart, FL). Visual stimuli were projected onto a screen at the back of the magnet bore, viewed by subjects through a mirror mounted on the MR head coil. Responses were made via button presses, using a fiber-optic button-box that registers latencies to the nearest millisecond. No stimulus was repeated within a subject to avoid repetition priming.

Behavioral Data Analysis

Reaction times (RTs) were measured from the onset of target display. RTs were computed for correct trials of each condition. Each participant's median RT for correct trials was entered into statistical analyses to minimize the effect of outliers. RTs were analyzed using analysis of variance (ANOVA) and t tests at the level of participants (F_1; t_1) and items (F_2; t_1).

MRI Acquisition

MRI data were collected on a 3-T Siemens Magnetom Trio MRI scanner. Foam padding was used to limit head motion within the coil. T2*-weighted functional images were acquired using the body coil to transmit and an eight-channel head array coil to receive. Main field B_0 homogeneity was optimized at the start of each run using an automated shimming routine. Functional image runs were acquired in the transverse plane using a gradient-echo, echo-planar imaging sequence (TE = 30 msec, TR = 2000 msec, flip angle = 77°). Thirty-eight interleaved slices were acquired (64 × 64 image matrix, 224 × 224 FOV, with isotropic 3.5 mm voxels), covering the entire cerebrum and the upper cerebellum. The experiment was divided into four runs, with each run containing 48 word targets (12 in each of the 4 conditions) and 24 pseudoword target trials presented in random order. An event-related design was employed, including trial types of interest and fixation trials (+) to create a baseline condition for analyses and to enable stimulus jittering. Different trial types of interest were separated from each other by a variable intertrial interval (ITI range = 0–10 sec, mean = 2.6 sec) consisting of baseline fixation. The ITI range and pseudorandom ordering schedule were customized for the present design using the optseq2 program (http://surfer.nmr.mgh.harvard.edu/optseq/), promoting optimal experimental efficiency (Dale, 1999). A high-resolution, 3-D anatomic image was acquired using a T1 weighted (MP-RAGE) sequence (TR = 2100 msec, TE = 2.93 msec, TI = 1100 msec, flip angle = 12°, FOV = 224 × 256 × 192 mm, 1 mm isotropic voxels, sagittal partitions) for the localization of functional activity in the stereotactic space of Talairach and Tournoux (1988).

fMRI Data Analysis

fMRI data were analyzed with AFNI software (Cox, 1996). A series of preprocessing steps were used to minimize artifacts. The first few functional volumes (12 sec) of each run were excluded from analyses due to T1 saturation effects. Differences in timing between slices due to acquisition order were then adjusted with sinc interpolation. Next, functional images were motion corrected and registered to the image collected closest in time to the high-resolution anatomical image using a six-parameter rigid body transformation (Cox & Jesmanowicz, 1999). Finally, functional images were smoothed spatially with a 4-mm root-mean-square (5.4-mm full width half maximum) Gaussian kernel and intensity normalized to yield subsequent activation measures expressed as percent signal change from baseline.

Deconvolution analysis was performed on each subject's preprocessed image time series to provide simultaneous parameter estimates of the hemodynamic response associated with each condition (Glover, 1999). Hemodynamic impulse response functions (IRFs) were estimated at eight 2-sec time lags (0–16 sec) after stimulus presentation for correct trials in each condition compared to baseline fixation. Trials in which incorrect responses occurred were coded as a separate condition and were included in the model as a nuisance covariate to increase statistical sensitivity. Additional nuisance

regressors included in the model were each run's mean and linear trend. Each subject's IRF dataset was then transformed to the standardized space of Talairach and Tournoux (1988), using landmarks from their anatomical datasets, and resampled at 1 mm^3 resolution using cubic spline interpolation.

During second-level analyses, group-based, voxelwise t tests were performed on IRF datasets from the deconvolution analysis using a mixed-effect model that treated condition as a fixed effect and participants as a random effect. A conservative conjunction approach was employed to identify priming effects within regions involved in word recognition. As a first step, the combined data from all visual word target conditions was contrasted with visual fixation to identify the broad network of regions involved in lexical decision. Monte Carlo simulations were run using AlphaSim in order to determine the significance level and number of contiguous voxels needed to be active in order to achieve a corrected significance level of $p < .05$. The Monte Carlo calculation used 10^4 trials. Ultimately, a voxel-level threshold of $p < 10^{-4}$ and a minimum cluster size of 8 contiguous active voxels were chosen to achieve a corrected significance level of $p < .05$. Within this distributed system involved in visual word recognition, voxels were then characterized by their response to different components of visual word recognition (as reflected by *decreased* blood oxygen level-dependent response in each priming condition compared to the unrelated condition) at a more liberal significance threshold ($p < .05$), and a cluster threshold of 8 contiguous voxels. Activation maps from different contrasts were projected onto a common surface using Caret software (Van Essen et al., 2001) to visualize common and distinct activation patterns.

Magnitude data were extracted to compare relative priming effect sizes. Masks were generated using the 3dcalc tool in AFNI and consisted of a three-dimensional area including all voxels ($p < .001$) within 10 mm of the peak of a unique or overlapping priming effect. These ROI masks were then applied to each subject's IRF dataset to extract mean magnitude estimates across all voxels in an ROI during each condition. Single averaged magnitudes within ROIs were submitted to statistical tests based on a mixed-effects model, treating condition as a fixed effect and participants as a random effect.

RESULTS

Task Performance

Mean accuracy was near ceiling for the morphological (94.1%), lexical–semantic (95.4%), orthographic (96.3%), and unrelated (96.1%) word conditions. Figure 2 presents average latencies to correct responses for morphological, lexical–semantic, orthographic and unrelated conditions, and average priming effect sizes (unrelated − related).

ANOVA indicated a significant difference in reaction time to targets preceded by unrelated, morphological, lexical–semantic, and orthographic primes [$F_1(3, 45) = 3.7$, $p < .05$; $F_2(3, 141) = 2.7$, $p < .05$]. Planned comparisons revealed a significant priming effect restricted to the morphological condition [$t_1(15) = 5.7$, $p < .001$; $t_2(47) = 2.5$, $p < .05$]. There were also trends toward priming for the orthographic [$t_1(15) = 1.7$, $p = .11$; $t_2(47) = 1.8$, $p = .06$], and lexical–semantic [$t_1(15) = 1.8$, $p < .09$; $t_2(47) = 1.7$, $p < .09$] conditions. Importantly, however, priming was larger for the morphological than for the orthographic condition [$t_1(15) = 2.2$, $p < .05$; $t_2(47) = 1.9$, $p = .06$], demonstrating that morphological priming effects could not be explained by mere overlap in visual form.

fMRI Data

Figure 3 displays the brain activation results for the comparison of all word conditions with baseline fixation. This comparison resulted in activation of a predominantly left hemisphere network of regions, including the occipito-temporal cortex, middle temporal gyrus, angular and supramarginal gyri, and inferior prefrontal cortex, consistent with previous functional neuroimaging studies of lexical decision (Hart, Kraut, Kremen, Soher, & Gordon, 2000; Rumsey et al., 1997).

Figure 2. Reaction times and priming effects. (A) Mean reaction times to targets preceded morphological (Mor), orthographic (Orth), lexical–semantic (Sem), and unrelated (Unrel) primes. (B) Mean priming effect sizes (unrelated − related) for targets preceded by each kind of prime. Vertical lines represent the standard error of the mean. Note: ***$p < .001$.
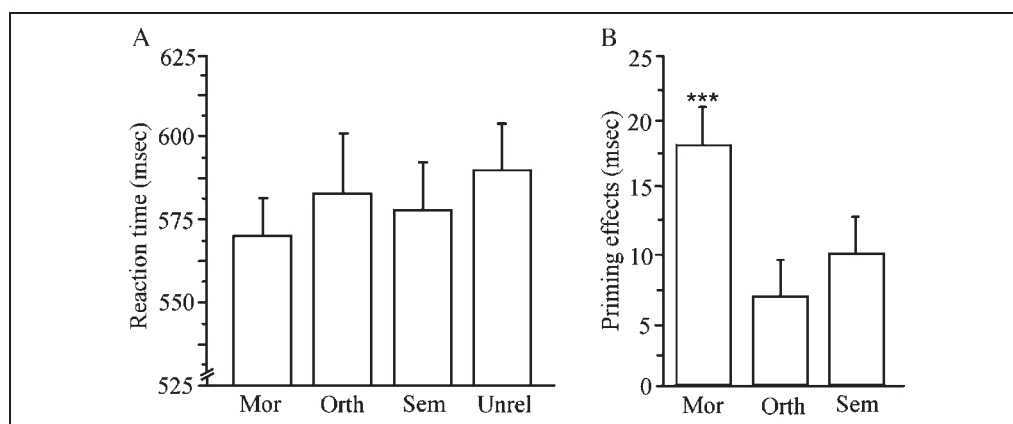
Figure 3. Lexical decision brain activations. Whole-brain maps comparing all word conditions (hot colors) with visual fixation (cold colors). Functional maps are projected onto semi-inflated surfaces. A network of predominantly left hemisphere regions is activated during lexical decision, including occipito-temporal and inferior frontal regions. The color bar displays the level of significance.
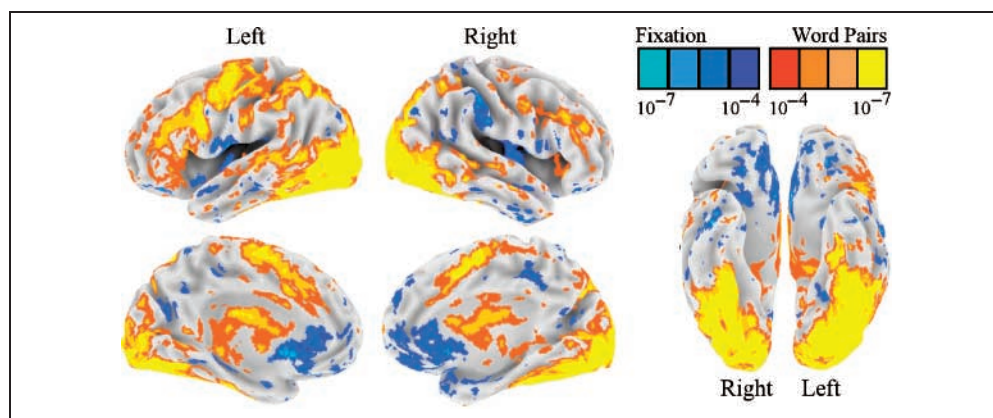
Within this lexical processing network, a small number of these regions showed a modulated response as a function of priming relationships (Figure 4 and Table 2). All priming effects were left lateralized. Orthographic priming was observed in two regions: an extrastriate region in the posterior portion of the middle occipital gyrus (P-MOG; ~BA 19) and a posterior portion of the fusiform gyrus (P-FFG; ~BA 37). Lexical–semantic priming was observed in one region: the middle temporal gyrus (MTG; ~BA 21). Like orthographic priming, morphological priming was observed in P-MOG and P-FFG. The morphological priming in these regions either overlapped, or consisted of voxels that were spatially contiguous with, orthographic priming effects. However, morphological priming was also observed in a third region that did not overlap either orthographic or lexical–semantic effects: an extrastriate region in the anterior portion of the middle occipital gyrus (A-MOG; ~BA 19).
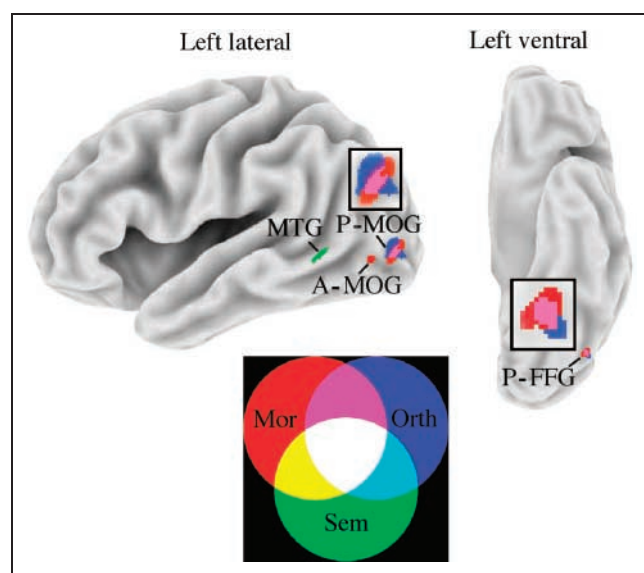
Region-of-interest (ROI) analyses were conducted to compare relative priming effect sizes. As can be seen in Figure 5, morphological and orthographic priming were not significantly different in either the P-MOG [$t(15) = 1.3$, $p = .23$] or the P-FFG [$t(15) = 0.61$, $p = .57$]. These regions showed sensitivity to orthographic structure, independent of morphology. In contrast, in the left MTG, lexical–semantic priming was greater than either orthographic priming [$t(15) = 4.1$, $p < .001$] or morphological priming [$t(15) = 2.2$, $p < .05$], demonstrating greater sensitivity in this region to semantics than morphology or orthography. Finally, in the A-MOG, morphological priming was greater than either orthographic priming [$t(15) = 2.9$, $p < .01$] or lexical–semantic priming [$t(15) = 3.7$, $p < .01$], demonstrating greater sensitivity in this region to morphology than orthography or lexical–semantics.

The unique morphological priming effect in A-MOG could be the result of the larger behavioral priming effect in this condition compared to other conditions. On this account, A-MOG could be sensitive to the size of any linguistic priming effect as opposed to morphological structure. To explore this possibility, we computed correlations between subjects' mean behavioral priming effects in each condition with their mean fMRI priming effects within A-MOG for the same condition. Results indicated a trend toward a relationship between morphological behavioral priming and morphological fMRI priming in A-MOG [$r(16) = .44$, $p = .08$], but not for orthographic behavioral priming and orthographic fMRI priming in A-MOG [$r(16) = .14$, $p = .52$] or lexical–semantic behavioral priming and lexical–semantic fMRI priming in A-MOG [$r(16) = .12$, $p = .57$]. The lack of correlation between orthographic and lexical–semantic behavioral priming and fMRI priming in A-MOG cannot be attributed to restricted variance in these conditions because the variance in behavioral priming was larger for these conditions than the morphological conditions (lexical–semantic = 80 msec; orthographic = 58 msec; morphologic = 42 msec) as was the variance in fMRI priming in A-MOG (orthographic = 0.048%; lexical–semantic =

Figure 4. Whole-brain MR priming effects. Whole-brain maps displaying regions activated by word pairs (hot colors in Figure 3) that also show priming effects.

Table 2. Talairach and Tournoux Activation Coordinates for Brain Regions that Showed Priming Effects

Region	BA	x y z (mm)	Cluster (μl)
Morphologic and Orthographic			
L Posterior middle occipital g. (P-MOG)	19	−40 −77 −1	318
L Posterior fusiform g. (P-FFG)	37	−48 −60 −17	57
Lexical–semantic			
L Middle temporal g. (MTG)	21	−54 −41 −2	87
Morphological			
L Anterior middle occipital g. (A-MOG)	~19	−37 −67 −7	53

Clusters reflect all contiguous voxels within a condition or overlapping the morphological and orthographic conditions. BA = approximate Brodmann's area; μl = volume; L = left; R = right; g. = gyrus.

0.046%; morphological = 0.038%). These results suggest that A-MOG is sensitive to morphological structure, as opposed to linguistic priming effect size more generally.

DISCUSSION

The present study used masked priming in conjunction with fMRI to evaluate recent claims suggesting the existence a form of morphological analysis within the visual word recognition system that operates independently of lexical–semantic information (Longtin & Meunier, 2005; Rastle et al., 2004; Longtin et al., 2003; Rastle & Davis, 2003). Prime–target pairs in our study shared a pseudo-morphological relationship (corner–CORN), a nonmorphological orthographic relationship (brothel–BROTH), or a lexical–semantic relationship (forest–TREE). Behavioral results demonstrated masked priming effects for the morphological condition, with trends for the orthographic and lexical–semantic conditions. These findings replicate recent results (e.g., Rastle et al., 2004; Longtin et al., 2003), suggesting a rapid form of morphemic segmentation that serves to decompose *any* letter string that has the appearance of morphological complexity (irrespective of its semantic characteristics). The present study provides a functional–neuroanatomic characterization of this morphological segmentation mechanism and its relationship to semantic and orthographic components of visual word recognition. The observed findings have clear implications for theories of morphological components of visual word recognition. Below we describe the priming effects associated with each condition and then discuss the implications of our findings for models of visual word recognition.

Lexical–semantic priming was observed in a portion of the left MTG (~BA 21). This result is consistent with

neuropsychological and functional neuroimaging studies, both of which have demonstrated a role for the MTG in lexical–semantic processing. For example, damage to the MTG is associated with poor recovery of comprehension (Naeser, Helm-Estabrooks, Haas, Auerbach, & Srinivasan, 1987). The MTG is activated during a range of different lexical–semantic tasks (Gold & Buckner, 2002; Binder et al., 1997; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996), and shows decreased response during semantic repetition priming (Gold, Balota, Kirchhoff, & Buckner, 2005; Raichle et al., 1994). In addition, short-term, automatic lexical–semantic linguistic priming has previously been demonstrated in this region (Copland et al., 2003).
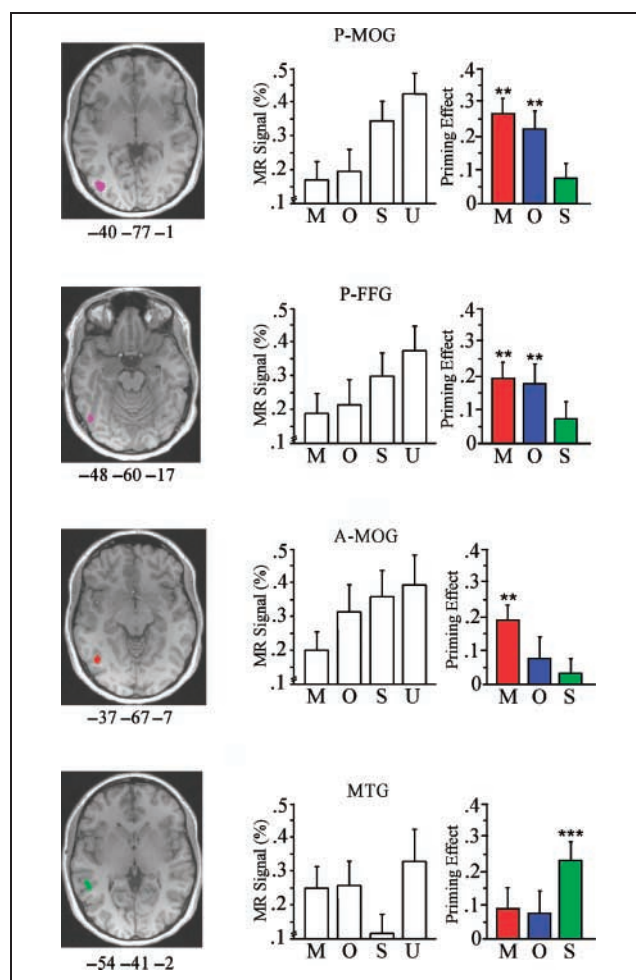

Figure 5. ROI MR priming effects. Priming effects in two regions showing overlapping orthographic and morphological priming (P-MOG and P-FFG), one region showing unique morphologic priming (A-MOG), and one region showing unique lexical–semantic priming. A representation of the location of each ROI is overlaid on a high-resolution image of a single subject in standardized space for identification on a traditional axial slice. Peak Talairach coordinates of ROIs are given under structural image. Bar charts display mean MR percent signal change from fixation for the morphological (M), orthographic (O), lexical–semantic (Sem), and unrelated (U) conditions. Colored bar charts show MR priming effects (unrelated > related) for the M, O, and S conditions. Note: **p < .01, ***p < .001.

In contrast, orthographic priming was observed in two more posterior left hemisphere regions: a posterior portion of the fusiform gyrus (P-FFG; ~BA 37), and an extrastriate region in a posterior portion of the middle occipital gyrus (P-MOG; ~BA 19). Both of these regions have been implicated in the processing of visual form. For example, neuropsychological evidence indicates that damage to large portions of the left occipito-temporal cortex can be associated with pure alexia, a unimodal deficit of word reading, with sparing of writing and auditory word comprehension (Binder & Mohr, 1992; Damasio & Damasio, 1983; Dejerine, 1892). More specifically, recent fMRI results have demonstrated a prominent P-FFG response in tasks associated with the processing of abstract letter units (Cohen et al., 2000, 2002) and have yielded neural priming effects in the P-FFG for an orthographic priming condition that included opaque morphological pairs (corner–CORN; Devlin et al., 2004). Similarly, the extrastriate region showing orthographic priming in our study (P-MOG) has shown greater response to alphabetic stimuli compared to checkerboards (Cohen et al., 2003) and significant activation related to orthographic components of visual word recognition (Rumsey et al., 1997). In addition, neural orthographic priming using partial word primes (ATL–ATLAS) has previously been demonstrated in the P-MOG (Gold et al., 2006).

Neural morphological priming did not overlap lexical–semantic priming but did overlap substantially with orthographic priming. Morphological priming was observed in both of the regions showing orthographic priming: P-FFG and P-MOG. There were voxels that showed unique morphological priming effects within each of these two regions. However, these morphological effects consisted of voxel clusters that were spatially contiguous with orthographic priming effects. To be conservative, these spatially contiguous clusters are reported as a single cluster, common to orthographic and morphological priming (see Table 1). The finding that morphological priming did not overlap lexical–semantic priming but did show substantial overlap with orthographic priming provides direct functional neuroanatomic evidence supporting the existence of a morphological segmentation mechanism that occurs independently of lexical–semantic processes, at an early structural level (Rastle et al., 2004; Longtin et al., 2003; Rastle & Davis, 2003). In addition, results also provide evidence that this early morphological decomposition process cannot be explained on the basis of orthographic (letter) similarity alone because there was one region that showed priming unique to the morphological condition.

Unique morphological priming was observed in the A-MOG (~BA 19). Unlike the spatially contiguous orthographic and morphological voxel clusters observed in the more posterior extrastriate region (P-MOG), the de-activation cluster in the A-MOG was clearly spatially distinct from that in the P-MOG, with peak decreases between the two regions separated by 1 cm. The A-MOG has been activated during many tasks involving high-level visual processing, including, but not limited to, object processing (Grill-Spector et al., 1999) and face processing (Gorno-Tempini et al., 1998). The A-MOG has also been activated during the naming of very rapidly presented words (Dehaene et al., 2001). The region therefore appears to be involved in numerous high-level visual processes and is not specialized for morphological processing. The important point with respect to the goals of the present study is that this region showed neural priming unique to the morphological condition in a single group of subjects who completed morphological, orthographic, and lexical–semantic conditions.

It is interesting to consider why the A-MOG showed morphological but not orthographic priming in the present study. One possibility is that this region did not show orthographic priming due to the small behavioral priming effect observed in this condition. However, the correlational analyses that we reported, along with the fact that robust neural orthographic priming was observed in two other regions, would seem to rule this possibility out. More likely is the possibility that the posterior-to-anterior, orthographic–morphological gradient of neural priming effects observed in this study reflects a general organizing principle of the occipito-temporal cortex: that the processing stream tends to proceed in the anterior direction as visual linguistic operations become more complex and abstract (McCarthy, Nobre, Bentin, & Spencer, 1995; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Nobre, Allison, & McCarthy, 1994). This notion is consistent with evidence from intracranial recordings that have suggested sensitivity to orthographic form in the posterior occipito-temporal cortex and sensitivity to lexical–semantic material in the mid-to-anterior occipito-temporal cortex (Nobre et al., 1994). Morphemes are clusters of letters that serve as functional units within words, and can therefore be regarded in a hierarchical framework as occupying a greater level of abstraction than letters themselves.

One interesting aspect of our data is that no fMRI suppression effects were observed in the left inferior prefrontal cortex (LIPC), despite neuropsychological and functional neuroimaging research suggesting that this region may be involved in morphological processing (Tyler, Marslen-Wilson, & Stamatakis, 2005; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Miceli et al., 2002). However, these studies all employed tasks that permit strategic processing, such as explicit morphological decision tasks or priming designs in which primes were subject to conscious appreciation, whereas our study used a masked priming paradigm in which participants were unaware of primes. Together, these findings raise the possibility that the LIPC contributes more prominently to later more strategic components of morphological analysis than earlier more automatic components. Future research will be required to explore this issue directly,

perhaps by studying morphological priming effects at different SOAs.

The pattern of fMRI suppression effects observed in the present study provides some neurophysiological constraints on theories of morphological segmentation during visual word recognition. Prime–target pairs with a pseudomorphological relationship (e.g., corner–CORN) yielded significant neural priming effects that (a) did not overlap at all with neural priming effects observed for pairs with a lexical–semantic relationship; (b) overlapped considerably with neural priming effects observed for pairs with an orthographic relationship; and (c) were unique to one region of the extrastriate cortex. These data are inconsistent with any morpho-semantic theory (whether localist or connectionist) in which morphology is described as a characterization of the form-meaning mapping (e.g., Giraudo & Grainger, 2000; Plaut & Gonnerman, 2000; Rueckl & Raveh, 1999) and in which morphological decomposition arises only in cases in which morphologically complex words are semantically related to their stems (Marslen-Wilson et al., 1994). Instead, these data support morpho-orthographic theories in which the sublexical orthographic representations used in visual word processing are themselves morphologically structured (Rastle et al., 2004; see also Taft, 1994; Seidenberg, 1987).

The early form of morphological segmentation that we have observed has been characterized in both classical-localist and distributed-connectionist frameworks, so it is worthwhile to consider briefly whether our data favor one or the other of these perspectives. Localist theories account for this type of decomposition in terms of an explicit level of morphological representation that resides between representations of letters and orthographic representations of whole words (Rastle et al., 2004; Taft, 1994). According to these theories, representations of "corner" would overlap those of "CORN" in both letter units and morpheme units, whereas representations of "brothel" would overlap those of "BROTH" only in letter units. This theory would therefore predict that morphological neural priming effects should overlap with pure orthographic neural priming effects in some brain regions due to shared letter representations of prime–target pairs in each condition. However, classical-localist theories would also predict morphological neural priming effects in brain regions distinct from those showing pure orthographic neural priming effects because morphological prime–target pairs share overlap in higher-level morphemic representations, whereas orthographic prime–target pairs do not. In general, this is the pattern of neural priming effects that we observed.

By contrast, distributed-connectionist theories of non-semantic morphological segmentation eschew the notion of explicit morphological representations. These theories argue instead that representations of orthographic form may develop a morphological structure as a result of the distinctive bigram and trigram frequency contours that characterize morphologically complex words (Rastle et al., 2004; Seidenberg, 1987).[1] Networks sensitive to this characteristic of morphologically complex words may come to represent these words componentially at the orthographic level, such that learned orthographic representations of "corner" and "CORN" would overlap to a greater degree than learned orthographic representations of "brothel" and "BROTH." As with localist theories, then, connectionist theories would predict that morphological neural priming effects should overlap with pure orthographic neural priming effects.

However, at least some (but not necessarily all) connectionist theories would also predict that neural morphological priming should be of a greater magnitude than neural orthographic priming in "orthographic regions" due to the greater orthographic similarity of morphological pairs (corner and CORN) than pure orthographic pairs (brothel and BROTH) that these theories posit. We found no evidence for such graded neural priming effects in "orthographic regions" in the present study. Rather, similar sized neural morphological and orthographic effects were observed in regions that showed overlapping neural priming effects. Finally, connectionist theories would also seem to have difficulty explaining neural morphological priming in a region not showing orthographic priming, a finding that was observed in the present study. On balance, therefore, it would appear that the localist theory of nonsemantic morphological segmentation provides a closer description to the pattern of neural priming effects that we observed.

In summary, the present study provides the first functional neuroanatomic evidence supporting the existence of an early form of morphological decomposition in visual word processing that operates on any letter string that has the appearance of morphological complexity. Three left-lateralized occipito-temporal regions showed sensitivity to early morphological components of visual word recognition. Two of these regions also showed orthographic priming ($\sim$BA 37, peak: -48 -60 -17; $\sim$BA 19, peak: -40 -77 -1), whereas one was sensitive only to morphological similarity between primes and targets ($\sim$BA 19, peak: -37 -67 -7). Brain regions sensitive to morphological structure were distinct from those sensitive to lexical–semantic similarity ($\sim$BA 21, peak: -54 -41 -2). These findings provide a neurobiological basis for a purely structural morphological segmentation mechanism operating at early stages of visual word recognition, providing support for morpho-orthographic theories of morphology (Rastle et al., 2004; Longtin et al., 2003).

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Note

1. These words typically exhibit a ''trough'' pattern in which bigram and trigram frequencies are much higher *within* morphemic units than *across* morphemic boundaries (see Rastle et al., 2004).

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