

Neural correlates of morphological decomposition during visual word recognition

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Abbreviated title: morphological decomposition

Figures and tables: Five figures and 2 tables

Number of pages: 33

Key words: masked priming, morphology, word recognition, brain activation,
fMRI

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 fMRI priming suppression to look for evidence of non-semantic morphological priming at the neural level. Both behavioral and fMRI 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 occipitotemporal 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 et al., 1990). The semantic component involves sensitivity to the meanings of letter strings that have a lexical status (Strain et al., 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 et al., 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 pseudo-morphological 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., Marslen-Wilson et al., 1994; Meunier & Longtin, in press; Rastle et al., 2000). This support has been restricted, however, 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 ms) 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 and, more recently, ERP studies using this paradigm have reported robust priming for pseudo-morphological 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 non-morphological form relationship (e.g., brothel-BROTH; -el never functions as a suffix in English; Lavric et al., in press; Longtin et al, 2003; Longtin & Meunier, 2005; Rastle & Davis, 2003; Rastle et al., 2004). 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 (Rastle et al., 2000; Rastle et al., 2004; Longtin et al., 2003; Longtin & Meunier, 2005). 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 fMRI suppression to look for evidence of pseudo-morphological priming at the neural level. Several fMRI experiments have reported reduced BOLD 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 ms) and relatively small behavioral priming effect size (~16 ms), robust fMRI suppression was observed in extrastriate and fusiform cortices of the left hemisphere. While 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 et al. (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 posterior occipitotemporal cortex) and semantic effects (in 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. (2004) consisted largely of pseudo-morphological pairs (e.g., corner-CORN). This study did not separate orthographic (e.g., brothel-BROTH) and pseudo-morphological 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 pseudo-morphological 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.

 Insert Figure 1 about here

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, et al., 1993). Many of the morphological and orthographic pairs were used in Rastle et al. (2004). Pairs in the pseudo-morphological condition were semantically opaque, sharing an apparent morphological relationship 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 non-morphological 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 4 word conditions.

Pilot Study

A pilot study was conducted to determine whether presentation of masked prime stimuli for 30 ms could be consciously perceived by participants. Twelve healthy volunteers participated (8 females, 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 ms forward mask (#####), a word or pseudoword presented in lowercase for 30 ms (e.g., corner, floop), and a backward mask consisting of a word presented in uppercase for 500 ms (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 or not 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 participant's fMRI data were not analyzed due to within-run movement that exceeded 2 millimeters in one or more directions. The reported results reflect data from the remaining 16 participants (9 females, 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 ms forward mask (#####), a prime in lowercase for 30 ms, a target in uppercase for 1200 ms, and a fixation cross for 270 ms (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 a pseudorandom order, with a fixation cross presented during a variable intertrial interval to enable fMRI jittering (see below).

Stimulus presentation and recording of responses was implemented with E-Prime software (Psychology Software Tools Inc., Pittsburgh PA), using an MRI compatible projection system (SilentVision SV-6011 LCD, Avotec Inc., 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 ms. 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 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 3T 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 8-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, EPI sequence (TE = 30 ms, TR = 2000 ms, flip angle = 77°). Thirty-eight interleaved slices were acquired (64 x 64 image matrix, 224 x 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 enable stimulus jittering. Different trial types of interest were separated from each other by a variable inter-trial 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, 3D anatomic image was acquired using a T-1 weighted (MP-RAGE) sequence (TR = 2100ms, TE = 2.93ms, TI = 1100ms, flip angle = 12° , FOV = 224x256x192 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 et al., 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 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 1mm³ resolution using cubic spline interpolation.

During second-level analyses, group-based, voxel-wise 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 was 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* BOLD 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).

 Insert Figure 2 about here

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 occipitotemporal cortex, middle temporal gyrus, angular and supramarginal gyri, and inferior prefrontal cortex, consistent with previous functional neuroimaging studies of lexical decision (Rumsey et al., 1997; Hart et al., 2000).

 Insert Figure 3 about here

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 middle occipital gyrus (P-MOG; ~BA 19) and a posterior portion of fusiform gyrus (P-FFG; ~BA 37). Lexical-semantic priming was observed in one region: 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).

 Insert Figure 4 about here

 Insert Table 2 about here

Region of interest 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 posterior portion of middle occipital gyrus (P-MOG), $t(15) = 1.3$ $p = .23$ or the posterior portion of fusiform gyrus (P-FFG), $t(15) = .61$ $p = .57$). These regions showed sensitivity to orthographic structure, independent of morphology. In contrast, in left middle temporal gyrus (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 anterior portion of the middle occipital gyrus (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.

 Insert Figure 5 about here

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 ms; orthographic = 58 ms; morphologic = 42 ms) as was the variance in fMRI priming in A-MOG (orthographic = .048%; lexical-semantic = .046%; morphological = .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 et al., 2003; Longtin & Meunier, 2005; Rastle & Davis, 2003; Rastle et al., 2004). Prime-target pairs in our study shared a pseudo-morphological relationship (corner-CORN), a non-morphological 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., Longtin et al., 2003; Rastle et al., 2004) 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 left middle temporal gyrus (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 MTG is associated with poor recovery of comprehension (Naeser et al., 1987). MTG is activated during a range of different lexical-semantic tasks (Vandenberghe et al., 1996; Binder et al., 1997; Gold and Buckner, 2002), and shows decreased response during semantic repetition priming (Raichle et al., 1994; Gold et al., 2005). In addition, short-term, automatic lexical-semantic linguistic priming has previously been demonstrated in this region (Copland et al., 2003).

In contrast, orthographic priming was observed in two more posterior left hemisphere regions: a posterior portion of fusiform gyrus (P-FFG; ~BA 37), and an extrastriate region in a posterior portion of 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 left occipitotemporal cortex can be associated with pure alexia, a unimodal deficit of word reading, with sparing of writing and auditory word comprehension (Dejerine, 1892; Damasio & Damasio, 1983; Binder and Mohr, 1992). 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 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 chequerboards (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 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 (Longtin et al., 2003; Rastle & Davis, 2003; Rastle et al., 2004). 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 an anterior portion of middle occipital gyrus (A-MOG; ~BA 19). Unlike the spatially contiguous orthographic and morphological voxel clusters observed in the more posterior extrastriate region (P-MOG), the deactivation cluster in A-MOG was clearly spatially distinct from that in P-MOG, with peak decreases between the two regions separated by one centimeter. 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). 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 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 occipitotemporal cortex: that the processing stream tends to proceed in the anterior direction as visual linguistic operations become more complex and abstract (Halgren et al., 1994; Nobre et al., 1994; McCarthy et al., 1995). This notion is consistent with evidence from intracranial recordings that have suggested sensitivity to orthographic form in posterior occipitotemporal cortex and sensitivity to lexical-semantic material in mid-to-anterior occipitotemporal 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 left inferior prefrontal cortex (LIPC), despite neuropsychological and functional neuroimaging research suggesting that this region may be involved in morphological processing (Miceli et al., 2002; Tyler et al., 2000a; Tyler et al., 2005b). 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 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 pseudo-morphological 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 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 Seidenberg, 1987; Taft, 1994)

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 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 while 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-

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)

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 non-semantic 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 occipitotemporal 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). Brain regions sensitive to morphological structure were distinct from those sensitive to lexical-semantic similarity (~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 (Longtin et al., 2003; Rastle et al., 2004).

Acknowledgements

This research was supported by National Institutes of Health grant DC007315. The authors thank Jeff Covell for help with data collection and Drs. Anders Andersen, David Powell, and two anonymous reviewers for helpful comments.

References

- Baayen RH, Piepenbrock R, & van Run H (1993) *The CELEX lexical database* [CD-ROM]. Philadelphia: University of Pennsylvania, Linguistic Data Consortium.
- Binder JR, & Mohr JP (1992) The topography of callosal reading pathways. A case-control analysis. *Brain* 115: 1807-1826.
- Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T (1997) Human brain language areas identified by functional magnetic resonance imaging. *J Neurosci* 17: 353- 362.
- Burgess C, Livesay K (1998). The effect of corpus size in predicting reaction time in a basic word recognition task: Moving on from Kucera and Francis. *Behav Res Methods Instrum Comput* 30: 272-277.
- Cohen MS (1997) Parametric analysis of fMRI data using linear systems methods. *NeuroImage* 6: 93-103.
- Cohen L, Martinaud O, Lemer C, Lehericy S, Samson Y, Obadia M, Slachevsky A, Dehaene S, (2003) Visual word recognition in the left and right hemispheres: anatomical and functional correlates of peripheral alexias. *Cereb Cortex* 12: 1313-33.
- Cohen L, Dehaene S, Naccache L, Lehericy S, Dehaene-Lambertz G, Henaff M et al. (2000). The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain* 123: 291-307.
- Cohen L, Lehericy S, Chochon F, Lemer C, Rivard S, Dehaene S (2002) Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain* 125: 1054 -1069.
- Copland DA, de Zubicaray GI, McMahon K, Wilson SJ, Eastburn M, Chenery HJ (2003) Brain activity during automatic semantic priming revealed by event-related functional magnetic resonance imaging. *Neuroimage* 20: 302-310.
- Cox RW (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research* 29: 162-173.
- Cox RW, Jesmanowicz A. (1999). Real-time 3D image registration for functional MRI. *Magnetic Resonance in Medicine* 42: 1014-1018.

- Dale, AM (1999). Optimal experimental design for event-related fMRI. *Hum Brain Map* 8: 109-114.
- Damasio AR, & Damasio H (1983). The anatomic basis of pure alexia. *Neurology* 33: 1573-1583.
- Davis MH (2004). Units of representation in visual word recognition. *PNAS*, 101, 14687-14688.
- Dehaene S, Naccache L, Cohen L, Le Bihan D, Mangin JF, Poline JB, Riviere D (2001) Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience Nat Neurosci.* 4: 752-8.
- Dejerine J (1892). Contribution à l'étude anatomo-pathologique et clinique des différentes variétés de cécité verbale. *Mem Soc Biol* 4: 61-90.
- Devlin JT, Jamison HL, Matthews PM, Gonnerman LM (2004) Morphology and the internal structure of words. *PNAS* 101: 14984-14988.
- Forster KI, & Davis C (1984) Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, & Cognition* 10: 680-698.
- Frost, R., Grainger, J., & Rastle, K. (2005). *Current issues in morphological processing*. New York: Psychology Press.
- Giraud H & Grainger J (2000) Effects of prime word frequency and cumulative root frequency in masked morphological priming. *Language and Cognitive Processes* 15: 421-444.
- Glover GH (1999). Deconvolution of impulse response in event-related BOLD fMRI. *NeuroImage* 9: 416-429.
- Gold BT, & Buckner RL (2002) Common prefrontal regions co-activate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron* 35: 803-812.
- Gold BT, Balota DA, Kirchoff BA, Buckner RL (2005) Common and dissociable activation patterns associated with controlled semantic and phonological processing: Evidence from fMRI adaptation. *Cerebral Cortex* 15: 1438-1450.
- Gold BT, Balota DA, Jones SJ, Powell DK, Smith CD, & Andersen AH (2006). Dissociation of automatic and strategic lexical-semantics: Functional magnetic

- resonance imaging evidence for differing roles of multiple frontotemporal regions. *The Journal of Neuroscience* 26: 6523-6532.
- Gorno-Tempini ML, Price CJ, Josephs O, Vandenberghe R, Cappa SF, Kapur N & Frackowiak RSJ (1998) The neural systems sustaining face and proper-name processing. *Brain* 121:2103-18.
- Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzhak Y, Malach R (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24: 187-203.
- Halgren E, Baudena P, Heit G, Clarke JM, Marinkovic K (1994) Spatio-temporal stages in face and word processing. 1. Depth-recorded potentials in the human occipital, temporal and parietal lobes. *Journal of Physiology (Paris)* 88: 1-50.
- Hart J, Kraut MA, Kremen S, Soher B, Gordon B (2000) Neural substrates of orthographic lexical access as demonstrated by functional brain imaging. *Neuropsychiatry Neuropsychol Behav Neurol* 13: 1-7.
- Lavric A, Clapp A, & Rastle K. (in press). ERP evidence of morphological analysis from orthography: a masked priming study. To appear in *Journal of Cognitive Neuroscience*.
- Longtin CM, Segui J, & Hallé PA (2003) Morphological priming without morphological relationship. *Language & Cognitive Processes* 18: 313-334.
- Longtin CM, & Meunier F (2005) Morphological decomposition in early visual word processing. *Journal of Memory and Language* 53: 26-41.
- Marslen-Wilson WD, Tyler LK, Waksler R, & Older L (1994) Morphology and meaning in the English mental lexicon. *Psychological Review* 101: 3-33.
- Martin A, Haxby JV, Lalonde FM, Wiggs CL, Ungerleider LG (1995) Discrete cortical Regions associated with knowledge of color & action. *Science* 270: 102-105.
- McCarthy G, Nobre AD, Bentin S, Spencer DD (1995) Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *J. Neuroscience* 15: 1080-1089.
- Meunier F & Longtin CM. (in press). Morphological decomposition and semantic integration in word processing. To appear in *Journal of Memory and Language*.

- Miceli G, Turriziani P, Caltagirone C, Capasso R, Tomaiuolo F, Caramazza A (2002). The neural correlates of grammatical gender: an fMRI investigation. *J Cogn Neurosci* 15: 618-628.
- Naeser MA, Helm-Estabrooks N, Haas G, Auerbach S, Srinivasan M (1987) Relationship between lesion extent in 'Wernicke's area' on computed tomographic scan and predicting recovery of comprehension in Wernicke's aphasia. *Archives of Neurology* 44: 73-82.
- Nelson DL., McEvoy, CL, Schreiber TA (1998). The University of South Florida word association, rhyme, and word fragment norms. <http://www.usf.edu/FreeAssociation/>.
- Nobre AC, Allison T, McCarthy G (1994) Word recognition in the human inferior temporal lobe. *Nature* 372: 260-263.
- Olson R, Wise B, Conners F, Rack J. (1990) Organization, heritability, and remediation of component word recognition and language skills in disabled readers. In Carr TH, Levy BA, eds. *Reading and its development: component skills approaches*. San Diego: Academic Press: 261-322.
- Plaut DC, Gonnerman LM (2000) Are non-semantic morphological priming effects incompatible with a distributed connectionist approach to language processing? *Language and Cognitive Processes* 15: 445-485.
- Rastle K, Davis MH, Marslen-Wilson WD, & Tyler LK (2000) Morphological and semantic effects in visual word recognition: A time-course study. *Language and Cognitive Processes* 2000 15: 507-537.
- Rastle K & Davis MH. (2003). Reading morphologically-complex words: some thoughts from masked priming. In Kinoshita S & Lupker SJ (Eds.) *Masked priming: State of the art*. Hove: Psychology Press.
- Rastle K, Davis MH, & New B (2004) The broth in my brother's brothel: Morpho-orthographic segmentation in visual word recognition. *Psychonomic Bulletin & Review* 11: 1090-1098.
- Rueckl JG, Mikolinski M, Raveh M, Miner C, & Mars F (1997) Morphological priming, fragment completion, and connectionist networks. *Journal of Memory and Language* 36: 382-405.

- Rueckl JG & Raveh, M. (1999). The influence of morphological regularities on the dynamics of a connectionist network. *Brain & Language*, 68, 110-117.
- Rumsey JM, Horwitz B, Donohue BC, Nace K, Maisog JM, Andreason P (1997). Phonological and orthographic components of word recognition. *Brain* 120: 739-759.
- Seidenberg MS. (1987). Sublexical structures in visual word recognition: Access units or orthographic redundancy? In M. Coltheart (Ed.), *Attention and performance 12: The psychology of reading*. Hillsdale, NJ: Erlbaum.
- Stanners RF, Neiser JJ, Herson WP, & Hall R (1979) memory representation for morphologically related words. *Journal of Verbal Learning & Verbal Behavior* 18: 399-412.
- Strain E, Patterson KE, & Seidenberg MS (1995). Semantic influences on word recognition. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 21, 1140-1154.
- Taft M. (1994). Interactive activation as a framework for understanding morphological processing. *Language & Cognitive Processes*, 9, 271-294.
- Talairach J, Tournoux P (1988) *Co-planar Stereotaxic Atlas of the Human Brain* (Stuttgart: Thieme).
- Tyler LK, Marslen-Wilson WD, Stamatakis EA (2005a) Differentiating lexical form, meaning, and structure in the neural language system. *PNAS* 102: 8375-8380.
- Tyler LK, Stamatakis EA, Post B, Randall B, Marslen-Wilson WD (2005b). Temporal and frontal systems involved in speech processing: An fMRI study of the past tense processing. *Neuropsychologia* 43: 1963-1974.
- Vandenberghe, R. Price, C., Wise, R., Josephs, O., and Frackowiak, R.S.J. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature* 383, 254-256.
- Van Essen DC, Dickson J, Harwell J, Hanlon D, Anderson CH Drury HA (2001) An integrated software system for surface-based analyses of cerebral cortex. *Journal of American Medical Informatics Association* 41: 1359-1378.
- Wiggs CL, Martin A (1998) Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology* 8: 227-233.

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

	Orth	Mor	Sem	Unrel	ANOVA
Target Length	4.79	4.79	5.00	4.81	F(3, 188) = 0.80, n.s.
Target Frequency	17731	16978	18676	14848	F(3, 188) = 0.17, n.s.
Target N	3.06	3.02	3.06	3.27	F(3, 188) = 0.21, n.s.
Prime Frequency	8393	9314	9869	7900	F(3, 188) = 0.08, n.s.
Shared Letters	4.79	4.79	1.10	0.16	F(3, 188) = 4.4, $p < .01$

Note—N; orthographic neighborhood; Frequency is per 100 million observations (Burgess and Livesay, 1998); all direct t-test comparisons between conditions were $p \geq 0.34$ for variables other than shared letters.

Table 2. Talairach & Tournoux activation coordinates for brain regions that showed priming effects

Region	~BA	X	Y	Z (mm)	Cluster (μ L)
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. Abbreviations: BA = approximate Brodmann's area; μ L = volume; L = left, R = right; g. = gyrus.

Figures

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-semantic, were unrelated, or were pseudowords.

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 occipitotemporal and inferior frontal regions. The color bar displays the level of significance.

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.

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: ** $p < .01$, *** $p < .001$.

Figure 1

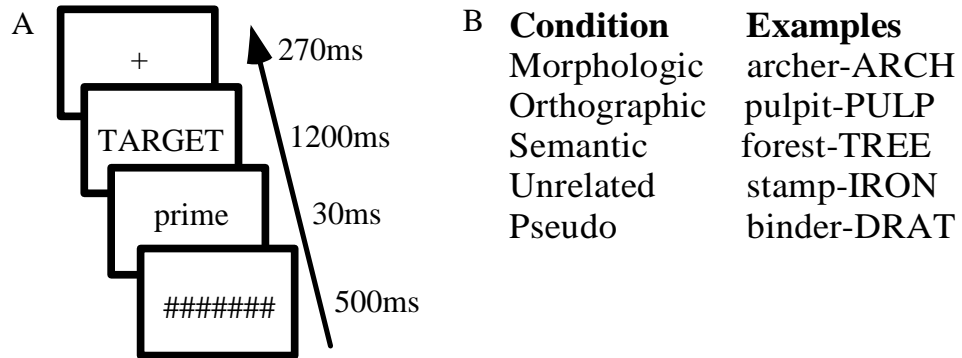


Figure 2

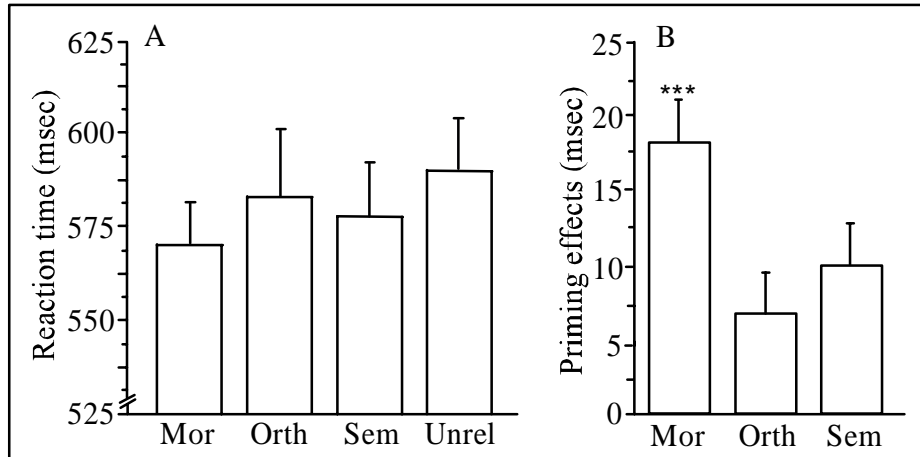


Figure 3

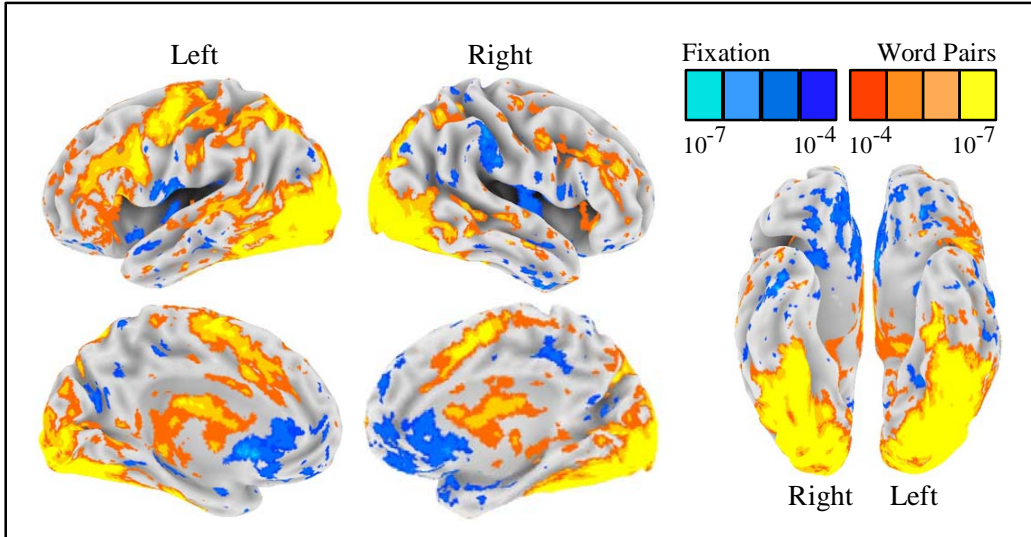


Figure 4

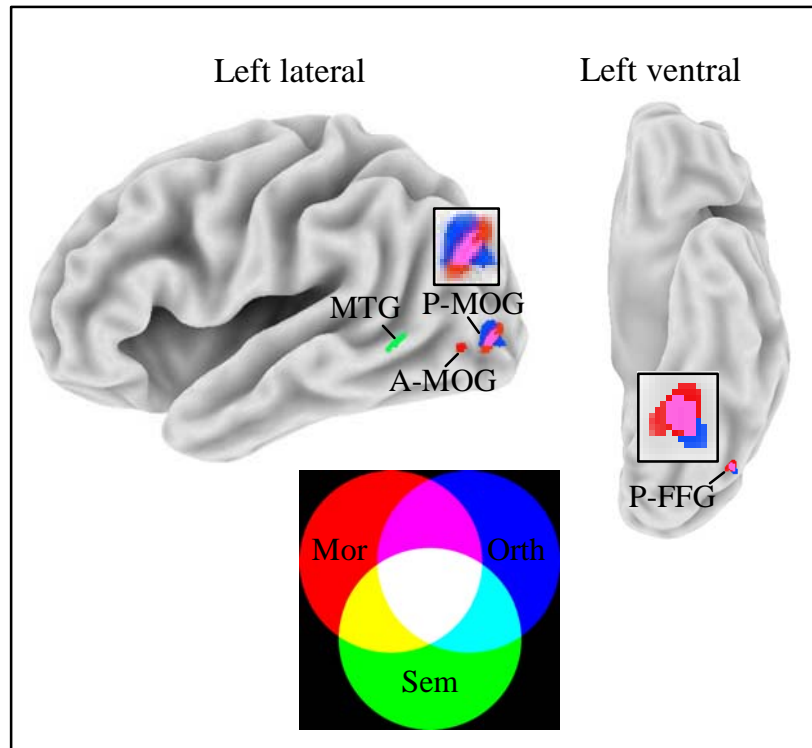


Figure 5

