Differentiating Morphology, Form, and Meaning: Neural Correlates of Morphological Complexity

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Abstract

The role of morphological structure in word recognition raises issues about the nature and structure of the language system. One major issue is whether morphological factors provide an independent principle for lexical organization and processing, or whether morphological effects can be reduced to the joint contribution of form and meaning. The independence of form, meaning, and morphological structure can be directly investigated using derivationally complex words, because derived words can share form but need not share meaning (e.g., archer–arch). We used an event-related functional magnetic resonance imaging paradigm to investigate priming between pairs of words that potentially shared a stem, where this link was either semantically transparent (e.g., bravely–brave) or opaque (e.g., archer–arch). These morphologically related pairs were contrasted with identity priming (e.g., mist–mist) and priming for pairs of words that shared only form (e.g., scandal–scan) or meaning (e.g., accuse–blame). Morphologically related words produced significantly reduced activation in left frontal regions, whether the pairs were semantically transparent or opaque. The effect was not found for any of the control conditions (identity, form, or meaning). Morphological effects were observed separately from processing form and meaning and we propose that they reflect segmentation of complex derived words, a process triggered by surface morphological structure of complex words.

INTRODUCTION

The adult speaker of a language like English can produce and comprehend tens of thousands of different words. Every word has a form—written and spoken—and a meaning. In addition, most words have a complex internal structure. The noun agreement, for example, can be analyzed into the morphemes agree and -ment, whereas the verb jumped contains the morphemes jump and -ed. A considerable body of psycholinguistic research suggests that the recognition of such words involves their decomposition into constituent morphemes (Longtin, Segui, & Hallé, 2003; Rastle, Davis, Marslen-Wilson, & Tyler, 2000; Marslen-Wilson, Tyler, Wakslar, & Older, 1994; Taft & Forster, 1975), prompting the question of the role of morphological structure in the word recognition process. More specifically, the question is whether morphemes function as organizational units in the mental lexicon and provide an independent principle for lexical organization and processing. The difficulty in answering this question comes from the fact that words that share morphological elements are usually also related in form and meaning and it is not straightforward to differentiate the effects of morphological relatedness from the contribution of form and meaning overlap.

The importance of this question relates to a major ongoing debate about the nature of linguistic knowledge as a neurocognitive phenomenon. Prominent connectionist views of language argue that the organization of language in the mind simply reflects statistical regularities in representations of form and meaning and in the mappings between these representations. Morphological structure itself has no independent status. Within this framework, effects of morphology are explained in terms of the joint effects of processing lexical form and meaning. Morphological structure is regarded either as a strictly epiphenomenal by-product of local regularities (Seidenberg & Gonnerman, 2000), or emerges out of these regularities in the form of implicit componential representations (Plaut & Gonnerman, 2000; Rueckl, Mikolinski, Raveh, Miner, & Mars, 1997). Consistent form-to-meaning mapping is crucial for this componential pseudomorphological structure to emerge. Items violating this consistency (e.g., department) will not be processed in a componential manner by a connectionist network, especially for languages like English with a relatively impoverished morphological system (Plaut & Gonnerman, 2000; Seidenberg & Gonnerman, 2000).

However, behavioral research seems to support, on balance, the view that morphology does have an independent role in lexical organization and processing: morphologically related words prime each other in the absence of priming for form and meaning across a
variety of different paradigms, including delayed repetition and masked priming (Frost, Forster, & Deutsch, 1997; Bentin & Feldman, 1990). In visual masked priming studies, which manipulate the time course with which different types of information become available during visual word recognition, priming for pairs of morphologically related words such as *happiness–happy* can be differentiated from the effects of orthographic overlap (*scandal–scan*) and meaning overlap (*battle–fight*) (Rastle et al., 2000). The claim for an independent role for morphological factors as distinct from form and meaning is strengthened by results showing robust priming between words that are potentially morphologically related, whether or not they are also related in meaning. For example, the words *department* and *depart* do not share the same underlying morpheme because the meaning of the stem *depart* is different in the two cases. Nevertheless, *department* is a potentially morphologically complex word in the sense that it consists of a stem (*depart*) and a legal affix (*ment*). In masked priming studies, pairs like this prime just as well as pairs like *happiness–happy*, suggesting an early morphological decomposition for all morphologically compositional words, which is blind to other factors (Longtin et al., 2003; Rastle et al., 2000).

The two competing approaches to the organization of the language system generate very different predictions for how morphological structure is neurally processed. If morphological structure is processed independently, we should be able to observe the neural consequences of morphological processing independent of form and meaning. In contrast, if morphological structure simply emerges as the joint contribution of form and meaning, there should be no neural activity for processing morphologically structured words as distinct from words that share form or meaning.

The existing evidence from neuroimaging and neuropsychology is mixed, as studies used different methods (e.g., different types of priming) and different types of morphological complexity (inflectional or derivational). Inflectional processes are morphosyntactic in nature: Combining stems and inflectional affixes (-ed, -s) generates grammatical variants of the stem (e.g., *jumped, cats*). Derivational processes are lexical: Adding derivational affixes (-ly, -ery) to stems forms new words (e.g., *bravely, writer*). A number of inflectional morphology studies have shown neural sensitivity to morphology (Tyler, Marslen-Wilson, & Stamatakis, 2005; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Dominguez, de Vega, & Barber, 2004; Tyler, Randall, & Marslen-Wilson, 2002; Laine, Rinne, Krause, Teras, & Sipila, 1999; Munte, Say, Clahsen, Schiltz, & Kutas, 1999; Marslen-Wilson & Tyler, 1998), whereas data from derivational morphology are scarce and inconsistent (Davis, Meunier, & Marslen-Wilson, 2004; Devlin, Jamison, Matthews, & Gonnerman, 2004; Pyllkänen, Feintuch, Hopkins, & Marantz, 2004). Although it cannot be excluded that neural correlates of morphological processes for inflections and derivations differ, we consider relevant evidence from both groups as they have one core property in common: Both types of words have complex morphological structure that may modulate their recognition processes and generate differential patterns of frontotemporal connectivity (Stamatakis, Marslen-Wilson, Tyler, & Fletcher, 2005).

Supporting the morphological account, a recent priming study on Spanish inflections compared event-related potential (ERP) responses to morphologically related words (e.g., *hijo–hija /son–daughter*) with the effects of semantic, orthographic, and homographic overlap (words with superficially similar stems but without any morphological or semantic relatedness, e.g., *foco–foca /floodlight–seal*). Only morphologically related words produced an attenuation of the N400, suggesting that morphology plays an independent role in lexical processing (Dominguez et al., 2004). Similarly, studies with brain-damaged patients have shown differential sensitivity to morphological structure that cannot be attributed simply to the effects of processing form and meaning. Patients with left frontal lobe damage show disrupted priming for word pairs whose processing requires morphophonological decomposition (e.g., regularly inflected past tense forms such as *jumped–jump*) but show normal priming for pairs that do not require such decomposition (e.g., *teach–taught, swan–goose*). The patients’ problems with regularly inflected pairs can be shown not to be reducible to general problems in form-based processing (Tyler et al., 2002).

Further neuropsychological evidence for functional differentiation between brain regions associated with processing morphological structure, form, and meaning comes from a recent study by Tyler, Marslen-Wilson, et al. (2005). Here, signal intensity across the entire brains of brain-damaged patients was correlated with behavioral priming scores for morphologically related regularly inflected past tense forms (e.g., *jumped–jump*), irregularly inflected past tense forms (*slept–sleep*), pairs related only in phonological form (e.g., *pillow–pill*) or in meaning (e.g., *card–paper*). The correlational analyses revealed that priming for regularly inflected forms was strongly associated with a network of left frontotemporal sites, in particular the left inferior frontal gyrus (LIFG). Damage to these regions had a significant impact on processing regularly inflected words but did not seem to affect the processing of irregularly inflected words and words related in form or meaning. This left frontal association with processing regular morphology is further supported by a functional magnetic resonance imaging (fMRI) study with healthy subjects (Tyler, Stamatakis, et al., 2005), where spoken regular pairs (*jumped–jump*) induced increased activation of frontotemporal regions compared to irregular pairs (*teach–taught*) or phonologically matched control pairs (*claim–clay*).

In contrast to these results, a recent fMRI study of derivational morphology found that neural priming for
morphologically related words was indistinguishable in location and extent from effects attributed to form and meaning overlap (Devlin et al., 2004). In this masked priming study, priming for morphologically related pairs (e.g., boldly–bold) was contrasted with priming for pairs that were intended to share only form (e.g., corner–corn) or meaning (e.g., idea–notion). Priming for morphologically related pairs compared to unrelated pairs (e.g., ozone–hero) was associated with reduced activation in three regions: left occipitotemporal, left middle temporal, and bilateral angular gyrus. However, this could not be uniquely attributed to morphological processing at any of these cortical locations because it could not be differentiated from orthographic processing in the occipitotemporal cortex, or from the interaction of orthographic and semantic processing in the middle temporal and the angular gyrus. A weakness of this study, however, was that the orthographic control condition in fact consisted of pairs like apartment–apart or homely–home, which are potentially decomposable into stems and affixes. Pairs like this show strong morphological priming effects in masked priming tasks (Rastle, Davis, & New, 2004; Longtin et al., 2005), in contrast to genuine orthographic controls, which were not used. The proper test for morphological independence requires the inclusion of a control condition in which the word pairs share form overlap but do not have a potential morphological structure (as in scandal–scan, where scandal cannot be decomposed into scan + dal because /dal/ is not a real suffix). Without this condition it is not possible to determine whether there are morphological effects independent of form overlap.

These diverging results may also reflect differences in methods used to look into the neural basis of morphological processing. Devlin et al. (2004) employed masked priming, which has been frequently used in behavioral studies of morphological processing. However, there is evidence that the neural effects of masked word primes are limited to posterior brain areas and largely reduced compared to fully visible primes (Dehaene et al., 2001, 2004), raising the possibility that masked priming may not engage morphological processing mechanisms in frontal regions. On the other hand, responses in immediate priming tasks (where both items from the pair are fully visible and presented in immediate succession) may induce strategies unless appropriate methodological controls are included.

In summary, previous neuroimaging and neuropsychological studies offer evidence both for and against independent morphological processing at the neural level, so that the overall picture remains unclear. In the present study, we tested the two competing accounts by comparing priming effects for sets of words organized along the dimensions of morphological, semantic, and orthographic relatedness. We focused on derived words because these offer the best opportunity for clearly dissociating the effects of morphology, form, and meaning.

Derivational processes add derivational affixes (–ness, –ment, –ly, –er) to stems to form new words that are either semantically transparent (e.g., brave–bravely, dark–darkness) or have a meaning that cannot be derived from the meaning of the constituent parts, as in semantically opaque items like arch–archer, depart–department, wit–witness (Marslen-Wilson et al., 1994). The contrast between semantically opaque and transparent derived words allows us to assess the effects of shared morphemes when semantic relatedness is either present or absent. To this end, the study included two morphological conditions, one in which the derived–stem pairs were semantically transparent (bravely–brave) and another in which they were semantically opaque (archer–arch). In both cases, the derived words could be segmented into a stem and a derivational affix. To avoid the confounds in previous studies (Devlin et al., 2004), we included a control condition in which word pairs were orthographically related but where the prime was not a potentially morphologically complex word because it could not be decomposed into a stem and an affix (e.g., scandal–scan, where /dal/ is not a real affix in English). There were two further control conditions: one where pairs shared meaning but not orthography or morphology (e.g., accuse–blame), and another with identical word pairs (e.g., mist–mist). Priming between identical repetitions of the same word can be based on whole word representations and does not require morphological analysis. To the extent that any activation due to morphological priming cannot be reduced to pure identity effects, or to semantic or form priming, this will support the claim that morphological structure is processed independently of form and meaning.

We used a delayed repetition priming task to maximize the distinction between the effects of morphology, form, and meaning, and avoid any potential problems associated with the use of masked and immediate priming paradigms. In delayed repetition task, subjects are presented with words for lexical decision, and the members of a word pair are separated by varying numbers of intervening words, which reduces the possibility that participants will employ strategies to perform the task. Previous studies using this task have shown that morphological priming is preserved over long lags, whereas semantic and form priming drop away sharply as the number of intervening items between prime and target increases (Bentin & Feldman, 1990; Napps, 1989). A simple baseline condition was also included, consisting of a single crosshair.

METHODS
Participants
Fifteen right-handed (6 men) native speakers of British English participated in the study. They had normal or
corrected-to-normal vision and had been screened for neurological or developmental disorders. All gave informed consent and were paid for their participation. The study was approved by the Addenbrookes NHS Trust Ethical Committee.

Stimuli

Prime–target word pairs were organized along the dimensions of morphological, semantic, and orthographic relatedness. The morphological status of the primes was determined using the CELEX English lexical database (Baayen, Piepenbrock, & Gulikers, 1995), and a modified version of the criteria set out in Marslen-Wilson et al. (1994). Pairs were deemed as morphologically related if (a) the derived form had a recognizable affix (as listed by Marchand, 1969) and (b) when the affix is removed, the resulting stem was a monomorphemic free form in the language. Semantic relatedness between prime and target was determined by means of a set of pretests, where participants rated a large set of word pairs on a 9-point scale, with 1 being not related at all in meaning and 9 being very related in meaning. Semantically unrelated pairs were rated between 1 and 3, whereas related pairs were rated between 6 and 9. In the conditions in which the prime and target shared form, targets were embedded in their primes at word onset (orthographically and phonologically), and amount of form overlap (i.e., the proportion of letters in a target relative to the number of letters in the prime) was matched across the conditions.

There were five conditions with 48 prime–target pairs each: (1) semantically unrelated pairs that potentially share a stem morpheme, where the remaining set of letters in the complex word is a legal suffix in English (opaque, e.g., archer–arch); (2) semantically and morphologically related pairs (transparent, e.g., bravely–brave); (3) pairs of simple words that are only semantically related (meaning, e.g., accuse–blame); (4) pairs sharing only form (form, e.g., scandal–scan). Pairs in this condition, although apparently sharing the stem (e.g., scan), are neither actually nor potentially morphologically related, because the remaining letters (e.g., the syllable dal) do not form a derivational affix in English and there is no linguistic basis for segmenting scandal into stem + affix; (5) identity pairs (half were simple words, mist–mist and half were complex lately–lately). Stimuli were closely matched in length, lemma frequency, neighborhood size, and semantic relatedness (semantic relatedness for opaque pairs, 2.0; for transparent pairs, 7.7; for meaning pairs, 7.7; and for form pairs, 1.6). These 240 real word pairs were interspersed with 160 nonword pairs and 160 baseline fixations. Nonword pairs were orthographically and phonologically legal sequences and their structure reflected the structure of the test conditions: In 20 pairs, nonword stems were embedded in nonwords that did not end in a potential suffix (e.g., barge–bar), 100 pairs were nonword stems embedded in nonwords with a real suffix (e.g., liscage–lisc, bleany–blean), and 40 were nonword pairs with no orthographic overlap (e.g., gheed–larm). The baseline condition was a single crosshair presented in the middle of the screen.

Stimuli were pseudorandomized with respect to type (words/nonwords/baseline) and condition, and members of the word pairs were presented, on average, 18 items apart. This corresponds to an average time interval of about 45 sec. Two lists including all the items were compiled, with order of presentation of words from the same pair counterbalanced across the lists (e.g., bravely–brave in List 1 and brave–bravely in List 2). In each list, half of the pairs from one condition were presented as stems following derived words and half as stems preceding derived words. Thus, each primed stem (e.g., brave primed by a prior presentation of bravely) could be compared with an unprimed stem from the same condition (e.g., lone), and these comparison stems were themselves the prime words for future targets (e.g., lonely). In this way each subject saw all the test items only once. The same procedure was used for nonword pairs, although with a wider distribution of repetition lags between related pairs. Using such an intrasubject design, we avoided potential confounds due to between-subject differences and, as there was no need to introduce an unrelated set of control items, maximized the amount of data obtained. The lists were divided into four blocks of 240 items each, containing equal numbers of items from each condition and each order of presentation.

Procedure

Stimuli were displayed for 400 msec, followed by a delay of 2 sec. They were presented in lower case in white on a black background on a video monitor ~1 m from the participants’ eyes. The same timing parameters were used for all stimuli. Stimulus presentation was controlled by the DMDX software (Forster & Forster, 2003) running on a Pentium II PC. Participants performed a lexical decision on each letter string and made no response to fixations, making the response with the right hand on a two-button response box. The order of the four blocks was pseudorandomized for each subject. Blocks were separated by short breaks.

Imaging Parameters

The study used an event-related design that enables us to assess neural responses to individual conditions that are presented in a pseudorandomized sequence. In this way, primed and unprimed trials are unpredictable to
participants so then, measured neural responses are unconfounded by strategies. Scanning was carried out on a 3T Bruker scanner at the Wolfson Brain Imaging Center, Cambridge. Blood oxygenation level dependent (BOLD) echo-planar images (TR = 1.1 sec, 21 slices, 4 mm thick with a 1-mm inter-slice gap, 128 × 128 in-plane resolution, 2 × 2 × 2 voxel size; 547 repetitions per session) were acquired obliquely, covering approximately the whole head. The first six scans of each time series were discarded to allow for steady-state magnetization before the test trials started. The event duration (2.4 sec) was not an integer multiple of the TR (1.1 sec) thus, echo-planar images were collected at various points along the hemodynamic response function (HRF) ensuring an effective sampling regime (Josephs, Turner, & Friston, 1997). Following the functional scans, structural T1-weighted spoiled gradient-recalled images were collected for anatomical localization.

The data were preprocessed and analyzed using SPM99 (Wellcome Institute of Cognitive Neurology, London, UK). Preprocessing involved slice time correction and image realignment to account for differences in slice acquisition times and correct for movement. The functional images were spatially normalized to the Montreal Neurological Institute reference brain and smoothed with an 8-mm isotropic Gaussian kernel to accommodate intersubject anatomical variability and to render the data suitable for statistical comparisons. The data for each subject were analyzed using the general linear model. Four sessions and 20 event types were entered in the model (primed and unprimed stems and derivations for each word condition, nonwords, and base-forms) were included to remove effects of residual movement on activation. Contrast images from each subject were combined into a group random effects analysis. SPMs were rendered at an uncorrected voxel threshold of $p < .001$ and we report maxima with a cluster size of $p < .05$ corrected for multiple comparisons and adjusted for the entire brain, unless otherwise stated. The peak coordinates for each cluster are reported in Talairach space. We used a nonlinear transform (Brett, Leff, Rorden, & Ashburner, 2001) to convert from MNI coordinates into the coordinate space of the brain in the Talairach and Tournoux (1988) atlas.

RESULTS

Behavioral Analysis

Reaction time data were inverse transformed to reduce the effect of outliers (Ratcliff, 1993) and entered into a mixed-design analysis of variance where we calculated $F_1$ (over subjects) and $F_2$ (over items). Lexical decision latencies were, on average, 14 msec faster for primed than for unprimed items [650 and 664 msec, respectively; $F_1(1,13) = 20.87, p < .01; F_2(1,406) = 14.51, p < .01$], with different priming effects across conditions [prime by condition interaction; $F_1(4,52) = 10.02, p < .01; F_2(2,406) = 3.09, p < .05$; Table 1]. Consistent with previous delayed repetition studies (Bentin & Feldman, 1990; Napps, 1989), we found significant priming in morphological and identity conditions [morphologically decomposable semantically opaque: 17 msec; $t(95) = 1.79, p < .05$; morphologically decomposable semantically transparent: 13 msec; $t(95) = 1.63, p = .05$; identity: 43 msec; $t(95) = 6.66, p < .01$]. Pairs related in either form or meaning did not prime [form: −10 msec, $t(95) = −1.10, p > .1$; meaning: 6 msec, $t(95) = 0.73, p > .1$].

To compare morphological effects with the effects of form and meaning, we combined the data from the two morphological conditions (opaque, archer–arch, and transparent, bravely–brave), and compared them with the combined effect of form (scandal–scan) and meaning (accuse–blame) overlap. Morphologically related pairs primed significantly [15 msec: $F_1(1,13) = 13.98, p < .01; F_2(1,176) = 5.79, p < .05$], whereas pairs related in either form or meaning did not $[-2$ msec; $F_1(1,13) = .15, p > .1; F_2(1,166) = .16, p > .1$], as reflected in a significant priming by morphological relatedness interaction [$F_1(1,13) = 13.23, p < .01; F_2(1,422) = 6.01, p < .05$]. Furthermore, morphologically related pairs primed irrespective of the semantic transparency of the items: There was no difference between the priming effect for opaque (e.g., archer–arch) and transparent (e.g., bravely–brave) conditions [priming by condition interaction, $F_1, F_2 < 1$].

Further analyses showed no significant differences in target facilitation in the stem–derived and derived–stem directions [priming by order interaction, $F_1, F_2 < 1$], and no significant changes in priming across the four sessions of the experiment [priming by session interaction, $F_1, F_2 < 1$].

<table>
<thead>
<tr>
<th>Condition</th>
<th>Primed RT (Error %)</th>
<th>Unprimed RT (Error %)</th>
<th>Priming (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Opaque</td>
<td>656 (6.5)</td>
<td>673 (4.8)</td>
<td>17*</td>
</tr>
<tr>
<td>Transparent</td>
<td>650 (2.7)</td>
<td>665 (5.5)</td>
<td>13*</td>
</tr>
<tr>
<td>Meaning</td>
<td>657 (4.5)</td>
<td>663 (4.8)</td>
<td>6</td>
</tr>
<tr>
<td>Form</td>
<td>676 (8.0)</td>
<td>666 (7.9)</td>
<td>−10</td>
</tr>
<tr>
<td>Identity</td>
<td>613 (2.7)</td>
<td>656 (4.0)</td>
<td>43**</td>
</tr>
</tbody>
</table>

*p < .05, statistically significant difference.

**p < .01, statistically significant difference.
p(F1,F2) > .1], suggesting that the observed effects were robust and temporally stable.

Imaging Analysis

We first determined the network of activated regions associated with reading written words. Comparing all letter strings against baseline revealed a network of primarily left hemisphere (LH) activity typically found in studies of written word recognition (Fiez & Petersen, 1998; Rumsey et al., 1997) (see Appendix for full description).

Our main analyses focused on the neural correlates of morphological complexity to determine whether they dissociate from the effects of form and meaning. Earlier research has highlighted the significance of the left inferior frontal regions in processing morphologically structured words and in morphological priming (Tyler, Marslen-Wilson, et al., 2005; Tyler, Stamatakis, et al., 2005; Tyler et al., 2002; Laine et al., 1999; Marslen-Wilson & Tyler, 1998) and we predicted the activation of left inferior frontal regions in our analyses. We first compared complex and simple words by contrasting activations due to the unprimed (first) presentation of morphologically decomposable semantically opaque and transparent words with the sets of the unprimed length-matched simple words from the form and meaning sets. The whole brain analysis revealed a single cluster of 39 voxels in LH pars orbitalis (Brodman’s area [BA] 47, peak at −40, 17, −13), significant after small volume correction (Z = 3.9, p < .01; Figure 1A) (SVC was performed on a 10-mm sphere following the predicted activation of this region for morphological processing, as noted above). The effect size plot in Figure 1A confirms that the first presentation of both opaque and transparent derived words produced significantly stronger activation compared to length-matched simple words. In contrast, comparing first presentation of simple words (stems) from the opaque and transparent conditions with length-matched simple words from the form and meaning set did not reveal any significant differences in this or any other region, suggesting that the LIFG is preferentially involved in processing morphologically structured words.

To determine whether there are any regions that show morphological priming distinct from priming due to overlap in form and meaning, we compared priming effects in the two morphologically related conditions (opaque and transparent) with those in the two morphologically unrelated conditions (form and meaning). This comparison produced a significant cluster of activation extending over the left inferior frontal operculum (BA 44), insula, rolandic operculum, and precentral gyrus (BA 6) (Table 2 and Figure 1B). The plot in Figure 1B confirms that this region showed reduced activation for the presentation of the second member of a pair of words, but only when...
Table 2. Regions of Significantly Reduced Activation for Second Presentation of Morphologically Related Words Compared to Second Presentation of Morphologically Unrelated Words

<table>
<thead>
<tr>
<th>Region</th>
<th>Extent</th>
<th>Coordinates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insula</td>
<td>100</td>
<td>3.73 −40 12 7</td>
</tr>
<tr>
<td>Rolandi操ularum</td>
<td>3.64</td>
<td>−51 2 11</td>
</tr>
<tr>
<td>Pars orbitalis (BA 47)</td>
<td>3.51</td>
<td>−38 15 −11</td>
</tr>
</tbody>
</table>

Statistics of the cluster are thresholded at .001, following whole-brain analysis.

there was a potential morphological relationship between prime and target. There was no reduction of activation for the second member of a pair for words related either by form or meaning. We also compared priming in the form condition with priming in the opaque condition to determine whether the observed effect in the LIFG is due to the processing of morphological structure even in the absence of semantic overlap. Morphological priming in the opaque condition was significantly greater than form priming in the LIFG, with no difference in the reverse direction in this region.

The nature of the identity condition allowed a further test of the hypothesis that the left inferior frontal regions are involved in processing morphologically structured words. Because half of the identity pairs were complex (e.g., lately–lately) and half simple (e.g., mist–mist), we compared priming effects for these two types of items. If the left frontal system is preferentially involved in processing complex items, we would expect greater neural priming for complex compared to simple identity pairs, reflected in a priming by complexity interaction for identity pairs. Because the number of items in each set was small, we thresholded this interaction at p < .01, and observed a cluster of 32 voxels with a peak in the pars triangularis (BA 45; −34, 22, 15), significant at .001 uncorrected voxel level (Z = 3.05). No reliable activation in the same region was observed for the reverse interaction (i.e., greater priming for simple items).

Figure 2 illustrates the overlap between the three sets of activations for morphologically structured words. All three activation clusters fall within the left inferior frontal region, with the effects of morphological priming overlapping both with activation for unprimed complex items as well as for the complexity by priming interaction for identity pairs. Taken together, these results provide consistent evidence for a key role of the LIFG in processing morphologically structured words, supporting and extending findings from previous results on inflected words (Tyler, Marslen-Wilson, et al., 2005; Tyler, Stamatakis, et al., 2005; Laine et al., 1999).

In a final set of analyses we looked at the effects of morphological priming across the four blocks of the experiment. There is evidence that regions of the LIFG play a role in response learning and adaptive decision making (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004), raising the possibility that the LIFG activation for morphologically complex words arises as a task-related effect, with subjects becoming increasingly aware of the relationship between morphologically structured words during the experiment. If the observed morphological priming is driven by this type of task-related effect we would expect to see an increase in priming over time. Paired t tests comparing priming effects across all subjects in the first and the final block produced no significant effects in the LIFG in any direction, suggesting their stability over time. To further examine the possibility of changes in priming effects over the four blocks, we performed a subjectwise linear regression on the weighted parameter estimate images expressing morphological priming effects with the block number as the regressor. Both whole-brain and region-of-interest (ROI) analyses (ROI defined as activation cluster from the morphology and priming interaction; Figure 2) showed no significant effects of block order.

**DISCUSSION**

The present study investigated the neural systems that process morphologically complex derived words, asking whether morphological complexity invokes neural activity that can be differentiated from processing lexical form and meaning. To this end we used a delayed repetition paradigm (Bentin & Feldman, 1990; Napps, 1989) and compared facilitation for morphologically related words to the effects for words that shared either form or meaning. Both the behavioral and imaging results showed clearly divergent response patterns for pairs that shared morphological structure and pairs that did not. Behaviorally, morphologically related words
primed each other, whereas morphologically unrelated words did not. Furthermore, the amount of priming for transparently related pairs (e.g., bravely–brave) and pairs that were only potentially morphologically related (e.g., archer–arch) did not differ.

The imaging data revealed that the LIFG was preferentially engaged by morphologically complex words and this was the only region that showed priming effects due to morphological relatedness between words. Activity in the LIFG was specific to morphological processing and was not observed for the control conditions (identity, form, or meaning). Furthermore, the same neural activity supported the analysis of morphologically transparent and opaque complex forms, with no significant activation differences between the two types of words.

Previous research on the neural basis of morphological processing has focused mainly on inflections and has shown that the LIFG is specifically engaged by the processing of inflected word forms (Tyler, Marslen-Wilson, et al., 2005; Tyler, Stamatakis, et al., 2005; Tyler et al., 2002; Laine et al., 1999; Marslen-Wilson & Tyler, 1998; Ullman et al., 1997). Neuropsychological studies have shown that patients with damage to the LIFG have specific deficits in processing regular forms and spared processing of irregular forms (Tyler et al., 2002; Marslen-Wilson & Tyler, 1998; Ullman et al., 1997). In healthy subjects, Munte et al. (1999) showed a modulation of ERP signals for regular past tense verbs primed by their present tense forms, which did not occur for the irregulars. In Finnish, Laine et al. (1999) showed significantly stronger activation for processing inflected as opposed to simple words in BA 44/45. Our results extend these earlier findings by showing preferential activation of the LIFG in processing morphologically complex derived words.

The main question prompting our research, however, was whether this activation can be uniquely attributed to morphological processing, or whether it can be explained in terms of the joint or separate contributions of form- and meaning-based processes, as argued by many proponents of connectionist models. On this latter account, effects of morphological priming observed in the LIFG should be explicable as a combination of orthographic and semantic priming. We found no evidence for this in our data: The LIFG showed significant priming only for morphologically related word pairs and not for form- or meaning-related pairs. Earlier, localist accounts (Marslen-Wilson et al., 1994) as well as connectionist accounts (Plaut & Gonnerman, 2000) of English morphology have predicted clear differences between priming for pairs that share morphology, form, and meaning (i.e., semantically transparent pairs like bravely–brave) and priming for pairs that share morphology and form, but not meaning (i.e., semantically opaque pairs, archer–arch). No such difference was observed in our data. Indeed, there was a nonsignificant trend for a greater priming effect for opaque than for the transparent items. Thus, given that neither form nor meaning relatedness facilitated target recognition, and that morphological priming was not affected by semantic transparency of the complex items, we propose that morphological priming in the LIFG reflects the operation of a neural system in which morphological structure is processed independently of form and meaning.

The results from the recent fMRI study by Devlin et al. (2004) are also consistent with this proposal, despite the authors’ conclusion to the contrary. Their comparison between morphological processing and form-based processing in fact contrasted the same kinds of stimuli as the opaque and transparent morphologically related conditions in our experiment. Using a different paradigm—masked rather than delayed repetition priming—Devlin et al. found separation between morphological and semantic effects in the left occipitotemporal cortex (see also Devlin, Jamison, Gonnerman, & Matthews, 2006). Although the authors did not find morphological effects in the LIFG, this may reflect their choice of experimental paradigm. In contrast, the present study did not show priming effects (morphological or otherwise) in posterior regions. The differences in patterns of activation between repetition priming paradigms varying in factors such as delay, modality, and awareness is an interesting topic for future investigation (Orfanidou, Marslen-Wilson, & Davis, 2006; Fiebach, Gruber, & Supp, 2005).

What do these data tell us about the recognition of morphologically structured words and the neural underpinnings of their processing? There is increasing behavioral evidence that the earliest stage of this recognition process involves the rapid, obligatory decomposition of visually presented words into their stems and potential affixes (e.g., Rastle et al., 2000, 2004; Longtin et al., 2003; Forster & Azuma, 2000; Taft & Forster, 1975). This process holds for all complex derived words, and seems to be blind to their semantic transparency or opacity. The critical factor seems to be the potential (and not actual) decomposability of the complex form—whether its surface structure consists of a stem and an affix, irrespective of the transparency of its meaning, suggesting that it is the morphological structure of complex words that crucially governs this decomposition process. It is likely that the posterior left fusiform peaks picked up in the Devlin et al. (2004, 2006) studies reflect the neural correlates of these early decompositional processes.

The next stage of the recognition process is conventionally assumed to involve access to stored lexical representations of word form and meaning, and there is considerable evidence, for languages like English, that this access process, and the representations that it targets, are highly sensitive to the semantic transparency of morphologically complex derived forms. A host of overt immediate repetition priming studies (where the target immediately follows an unmasked prime) show
no priming for opaque pairs (*archer–arch*) but strong priming for transparent pairs (*bravely–brave*) (Feldman, 2000; Rastle et al., 2000; Feldman & Soltano, 1999). Inappropriate morphological segmentation, for example, of *archer* into *arch* + *er*, must be filtered out at this stage, if the recognition process is to have the correct outcome.

The behavioral and the imaging results from our study clearly demonstrate that early decomposition, whether inappropriate or not, has long-term consequences for the neural systems (and cognitive processes) that operate downstream from these early processes. The fact that the long-lag priming effects we see here do not differentiate between semantically transparent and opaque complex items suggests a link to segmentation processes that occur early on during word recognition and that are prelexical in nature (Longtin & Meunier, 2005). The long-lag repetition paradigm is unlikely to be picking up the transient segmentation processes occurring tens of milliseconds after a word is presented, and the main location of the effects that we see are in quite different, much more anterior brain areas.

What is striking is that these effects are observed at time intervals of 45 sec or more, long after immediate processing of the prime word had been completed, and long after the inappropriate decomposition of the opaque words would apparently have been discarded by the system. This is consistent with another recent long-lag study (Rueckl & Galantucci, 2005) that also showed evidence of morphological influences on early, prelexical stages of word recognition. The interesting question of course is what happens in this delay between primes and targets? We can only speculate, as the answer to this question crucially requires information about time course of the effects, which is not available from the fMRI paradigm used here.

One possibility is that presentation of the prime word involves the formation of an episodic memory trace (Wagner, Koustaal, & Schacter, 1999; Bueckner & Koustaal, 1998) that will resonate with the subsequently presented target even if there is no conscious recognition of the relationship between the prime and the target. If the prime word is morphologically complex (e.g., *bravely*), the word will be decomposed into the constituent morphemes (*brave* + *ly*), and the structure of its episodic memory representation will reflect this analysis. This leads to faster responses to the target *brave*. More importantly, the same process could hold for words such as *archer*. Although the *arch* + *er* analysis is subsequently rejected, it nevertheless creates a memory trace that incorporates *arch* as a component. By the time that *arch* is subsequently presented, the system has long forgotten that this was an episodic record of an incorrect analysis of the stimulus, and hence, resonance will still occur. This might also explain why there is no immediate priming for these pairs. As the target *arch* is presented, the system might be in the process of rejecting the decomposed analysis of the prime, thus highlighting the fact that the link between the prime and the target is spurious. One challenge for this episodic hypothesis, though, is a recent fMRI finding that long-lag repetition priming effects for spoken words appear to be unrelated to neural responses in brain regions traditionally associated with episodic memory (Orfanidou et al., 2006).

An alternative hypothesis is based on the assumption that processing morphologically complex words involves combinatorial processes that integrate morphemes into coherent lexical representations (Marslen-Wilson & Tyler, 1998; Tyler & Marslen-Wilson, 1998). Activity in the LIFG may reflect these combinatorial processes that operate on information received from previous processing stages. According to this hypothesis, early automatic morphological decomposition in posterior regions segments words with complex morphological structure into their potential constituent morphemes (consistent with the results of Devlin et al., 2004, and a proposal by Jobard, Crivello, & Tzourio-Mazoyer, 2003). This process is insensitive to the semantic properties of complex words and applies equally to semantically transparent words like *bravely* and semantically opaque words like *archer*. Consequently, any subsequent processing must work on the results from this early automatic process before words can map onto their corresponding lexical representations. Activation in left inferior frontal regions may reflect combinatorial operations on the output of this earlier processing stage, prior to their mapping onto stored lexical representations. Such processes are necessary in order to integrate the segmented output and would apply to all structurally compositional words that have previously been decomposed.

Thus, although the precise mechanisms of this process are still not clear, we propose that the LIFG activation we observed reflects consequences of an early mechanism that isolates potential morphemes whenever the structure of the complex words allows such a procedure. This prelexical morphological decomposition is sensitive to morpho-orthographic properties of the complex words, but not reducible to form alone. Further data from techniques sensitive to fine-grained temporal events, such as magnetoencephalography or electroencephalography, are required to pinpoint the exact timing of this process.

In summary, the results of this study show that morphological structure evokes a response of the left inferior frontal system. This activation seems to be separate from processing form and meaning, and we propose that it reflects a segmentation of complex derived words during visual word recognition, triggered by their surface morphological complexity. Our results extend previous accounts on the role of the left inferior frontal system, suggesting that this region supports structural processing of morphologically complex sequences.
APPENDIX

Significant activations for the contrast of all letter strings (words + nonwords) minus baseline. Statistics of the cluster are shown thresholded at .001, following whole-brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface.

<table>
<thead>
<tr>
<th>Regions</th>
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<th>Voxel Level</th>
<th>Coordinates</th>
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<td>$P_{\text{corrected}}$</td>
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Note

1. There was no stem-derived distinction in the meaning condition. Prime–target pairs in the identity condition were defined as derived–derived and stem–stem.

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