

Neurobiological Systems for Lexical Representation and Analysis in English

Mirjana Bozic^{1,2}, Lorraine K. Tyler¹, Li Su^{1,2}, Cai Wingfield²,
and William D. Marslen-Wilson^{1,2}

Abstract

■ Current research suggests that language comprehension engages two joint but functionally distinguishable neurobiological processes: a distributed bilateral system, which supports general perceptual and interpretative processes underpinning speech comprehension, and a left hemisphere (LH) frontotemporal system, selectively tuned to the processing of combinatorial grammatical sequences, such as regularly inflected verbs in English [Marslen-Wilson, W. D., & Tyler, L. K. Morphology, language and the brain: The decompositional substrate for language comprehension. *Philosophical Transactions of the Royal Society: Biological Sciences*, 362, 823–836, 2007]. Here we investigated how English derivationally complex words engage these systems,

asking whether they selectively activate the LH system in the same way as inflections or whether they primarily engage the bilateral system that support nondecompositional access. In an fMRI study, we saw no evidence for selective activation of the LH frontotemporal system, even for highly transparent forms like *bravely*. Instead, a combination of univariate and multivariate analyses revealed the engagement of a distributed bilateral system, modulated by factors of perceptual complexity and semantic transparency. We discuss the implications for theories of the processing and representation of English derivational morphology and highlight the importance of neurobiological constraints in understanding these processes. ■

INTRODUCTION

A fundamental property of human language is its generative capacity, whereby an infinite range of communicative meanings can be expressed using the combination and recombination of a finite set of linguistic elements. Here we focus on combinatorial processes realized at lexical and morphological levels, where different morphemes—typically a stem morpheme (e.g., *sad*, *jump*) and a bound grammatical morpheme (e.g., *-ness*, *-ed*)—combine to create new surface forms (*sadness*, *jumped*), and where a basic distinction is made between *inflectional* and *derivational* processes. Inflectional morphology subserves primarily grammatical functions, whereas derivational morphology is associated with the creation and representation of new words in the language. From a novel neurobiological perspective, which relates human language functions to two distinct underlying brain systems (Bozic, Tyler, Ives, Randall, & Marslen-Wilson, 2010; Marslen-Wilson & Tyler, 2007), we ask whether derivational morphology engages a specialized left hemisphere (LH) system, in the same way as inflectional morphology, or whether it engages domain general bilateral systems associated with nondecompositional access.

Neurobiological Systems for Language Comprehension

A substantial body of evidence suggests that spoken word comprehension engages a network of bilateral temporal and frontal brain regions (Bozic et al., 2010; Marslen-Wilson & Tyler, 2007; Beeman, 2005; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Binder et al., 2000). This global network can be broken down into two complementary systems with differential functional roles: a bi-hemispheric system, which supports sound-to-meaning mapping and general perceptual demands associated with word comprehension and an LH frontotemporal system, supporting grammatical computations (Bozic et al., 2010; Tyler & Marslen-Wilson, 2008; Marslen-Wilson & Tyler, 2007).

Support for this hypothesis comes from converging results of neuroimaging and neuropsychological studies. Contrasted with nonspeech acoustic baselines, spoken words activate bilateral regions in the superior and middle temporal lobes, which have long been associated with access from the speech stream to representations of lexical form and meaning (e.g., Wright, Stamatakis, & Tyler, 2012; Hickok & Poeppel, 2007; Tyler et al., 2005; Binder et al., 2000). Consistent with a bilateral distribution of these functions, patients with damage to left frontal and superior temporal regions (and spared right hemisphere equivalents) exhibit a relatively intact ability to recognise simple spoken words (e.g., *dog*, *house*) and show semantic priming effects comparable with those of healthy controls

¹University of Cambridge, ²MRC Cognition and Brain Sciences Unit, Cambridge

(Longworth, Marslen-Wilson, Randall, & Tyler, 2005; Tyler et al., 2002). Furthermore, word recognition supported by the right hemisphere is maintained even during acute LH disruption (Hickok et al., 2008), suggesting that it is underpinned by existing bilaterally supported capacities and is not a result of longer-term compensation due to neural plasticity and functional reorganization. In terms of the specific functions of this system, Bozic et al. (2010) show that it is sensitive to variations in the perceptual complexity of morphologically simple spoken words. The presence, for example, of an onset-embedded stem (e.g., *clay* in *claim*) triggers competition and increases the processing demands required for selection of the correct candidate, modifying frontotemporal activity bilaterally. Taken together, the existing evidence points to a bilateral system that underpins the general perceptual demands associated with whole-word, stem-based lexical access.

In contrast, a parallel set of results point to an LH network selectively tuned to the processing of linguistically complex sequences, whose combinatorial structure requires parsing and segmentation during language comprehension (cf. Marslen-Wilson & Tyler, 2007). Neuroimaging data consistently relate LH temporal, inferior frontal, and inferior parietal regions to the processing of syntactic and morphological complexity, where simple linguistic elements combine into more complex morphosyntactic structures (Hagoort, 2005; Shtyrov, Pihko, & Pulvermüller, 2005; Tyler et al., 2005; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003). Converging evidence from neuropsychology and neuroimaging reveals a close relationship between this LH circuit and regular inflectional morphology. English-speaking patients with left frontotemporal damage typically exhibit long-term disruption of comprehension and production of inflectionally complex words such as *played* or *jumped* (Tyler et al., 2011; Longworth et al., 2005; Goodglass, Christiansen, & Gallagher, 1993), where lexical access requires morpho-phonological parsing that breaks these forms down into their component morphemes (*{play}* + *{-ed}*).

The neurocognitive properties of regular inflectional morphology (although chiefly studied in English) are consistent with the defining properties of inflectional morphology cross-linguistically (Bickel & Nichols, 2007; Marslen-Wilson, 2007). First, inflectional morphology does not, by definition, create new words with new meanings that require new lexical entries. Inflectional variants like *cat* and *cats* or *walk* and *walked* are not listed as separate headwords in standard dictionaries, and the meaning of these forms is fully predictable from the meaning of the stem combined with the grammatical properties of the inflection. Second, inflections are responsive, in a regular and predictable way, to the properties of the grammatical environment in which they occur (e.g., Bickel & Nichols, 2007; Anderson, 1992). This is clear, for example, where inflectional morphemes express agreement—as in the third person singular *{-s}* for English verbs (*he walks*) or when morphological case is used to express the grammat-

ical role of a noun as subject or object in case-marking languages. The information carried by the inflection is not just about the stem itself, but about the phrasal and sentential interpretation to which that stem relates. This compositionality and contextual dependence of regularly inflected forms is consistent with a neurocognitive model where inflectional morphemes are stripped from their stems early in processing and where the grammatical information they carry engages the combinatorial linguistic mechanisms supported by LH peri-sylvian brain regions (Marslen-Wilson & Tyler, 2007).

Derivationally complex forms, although also constructed by combining a stem with a grammatical morpheme, seem to have quite different linguistic properties. Whereas inflectional morphemes result in different forms of the same word, adjusted to the requirements of its current phrasal and sentential environment, derivational processes produce new words—in linguistic terms, new lexemes with new lexical entries (Matthews, 1991)—whose meaning and syntactic function is much more context independent. The meaning of these words is less predictable from the simple combination of the meaning of their constituent morphemes. This lack of compositionality—and the range of variation from opaque forms like *department* to transparent forms like *bravely*—has prompted longstanding controversies in the psycholinguistic literature as to whether derived words are represented and processed with respect to their constituent morphemes or as whole forms with no underlying representation of their morphological structure (e.g., Baayen, Milin, Filipovic-Durdevic, Hendrix, & Marelli, 2011; Marslen-Wilson, Bozic, & Randall, 2008; Longtin & Meunier, 2005; Taft, 2004; Clahsen, Sonnenstuhl, & Blevins, 2003; Bertram, Schreuder, & Baayen, 2000; Rastle, Davis, Marslen-Wilson, & Tyler, 2000; Baayen, Dijkstra, & Schreuder, 1997; Schreuder & Baayen, 1995; Marslen-Wilson, Tyler, Waksler, & Older, 1994).

None of these accounts, however, systematically relate their hypotheses to the neural systems that underlie language function more generally. Nor does the current neuropsychological or neuroimaging literature provide an easily interpretable or consistent view of derivational processes, with studies varying in language (English, Italian, German, Finnish), input modality (visual or auditory), experimental tasks, and neuroimaging methods, as well as looking at both comprehension and production (e.g., Leminen et al., 2011; Meinzer, Lahiri, Fleisch, Hannemann, & Eulitz, 2009; Hamilton & Coslett, 2008; Marangolo & Piras, 2008; Bozic, Marslen-Wilson, Stamatakis, Davis, & Tyler, 2007; Vannest, Polk, & Lewis, 2005; Davis, Meunier, & Marslen-Wilson, 2004; Marslen-Wilson & Tyler, 1998; Badecker & Caramazza, 1991).

English Derivational Morphology in Its Neurobiological Context

Here we ask a specific, neurobiologically framed question about the processing and representation of derivationally

complex words in English. Do they exhibit the same neurocognitive characteristics as regular inflected forms, being processed compositionally in terms of their component morphemes, or are they primarily processed as stored whole forms, not requiring morpho-phonological parsing and segmentation as part of the access process?

Decomposition, Transparency, and Productivity

If decompositional accounts are correct, then the scope of decomposition is likely to be affected by two variables thought to influence the representation and processing of derived words. These are semantic transparency—how far the meaning of the stem is preserved in the derived form—and suffix productivity (e.g., Bertram et al., 2000; Marslen-Wilson et al., 1994). Psycholinguistically, the role of semantic transparency has been well established since the work of Marslen-Wilson et al. (1994), showing that there is strong cross-modal priming between semantically transparent pairs like *bravely/brave*, but not between semantically opaque words like *archer/arch*. Cross-modal priming reflects the properties of central lexical representations and suggests that the representation of semantically transparent forms preserves their underlying morphological structure (Marslen-Wilson, 2007; Clahsen et al., 2003).

The second variable, suffix productivity, is a measure of whether a suffix is currently in use to create new words in the language (Plag, 2006; Baayen & Lieber, 1991; Bauer, 1983). Productive suffixes (*-er*, *-ness*) are frequently used to coin new words in modern English (e.g., *birther*, *bubness*), compared with unproductive suffixes (*-ic*, *-th*), which have generally fallen out of use. Marslen-Wilson, Hare, and Older (1993) showed robust cross-modal priming between word pairs sharing a derivational suffix (e.g., *toughness/darkness*), but only when the suffix was productive—indicating that productive suffixes are more likely to be segmented and have separate, primable representations. More recently, Ford, Davis, and Marslen-Wilson

(2010) used lexical decision to show that decompositional effects are only obtained for derived words with productive suffixes. These considerations suggest that complex words with productive suffixes are more likely to be stored and processed in terms of their constituent morphemes.

By manipulating transparency and productivity, we can both evaluate their role in a neurobiological context and construct stimulus sets where these factors are appropriately controlled. Our first set of words (Table 1) contains transparent derived forms with productive suffixes (e.g., *bravely*). These consist of a stem whose meaning is transparently preserved in the whole form, combined with a highly productive suffix: $\{-ly\}$, for example, applies semi-paradigmatically to almost all adjectives in the language. These derivational forms are most similar to regular inflectional forms such as *played* and most likely to be stored in a decompositional format. These are contrasted with three other morphologically complex sets varying in transparency and productivity, ranging from transparent words with nonproductive suffixes (e.g., *warmth*), opaque words with productive suffixes (e.g., *archer*), to opaque words with nonproductive suffixes (e.g., *breadth*). Two sets of morphologically simple words complete the six conditions: words with a potential embedded stem but no suffix (e.g., *scandal*, where *dal* is not a suffix in English) and simple words, such as *giraffe*, with neither a potential embedded stem nor a suffix.

We test this set of conditions in an fMRI study that exactly parallels in methods and design the earlier Bozic et al. (2010) study. This showed strongly selective activation of the left-lateralized decompositional system by regularly inflected forms such as *played*. If derivationally complex forms in English engage the same LH system, then we expect to see a similar pattern here. If the likelihood of decomposition for derived words is tied to semantic transparency and suffix productivity, then selective LH activation will be seen most strongly for the transparent and productive *bravely* set. However, on

Table 1. Stimulus Properties

Condition (Example)	Stem Properties				Suffix Properties		
	Embed Stem	Relatedness Pretest	COALS	Freq Ratio	Suffix	Productivity	Hapax
1. Transparent/productive (<i>bravely</i>) +S+M+P	Yes	7.7	0.24	1.9	Yes	Productive	0.09
2. Transparent/non-productive (<i>warmth</i>) +S+M-P	Yes	7.5	0.26	2.7	Yes	Nonproductive	0.02
3. Opaque/productive (<i>archer</i>) +S-M+P	Yes	2.2	0.06	2.1	Yes	Productive	0.07
4. Opaque/nonproductive (<i>breadth</i>) +S-M-P	Yes	1.7	0.03	1.9	Yes	Nonproductive	0.03
5. Stem only (<i>scandal</i>) +S-M P ₀	Yes	1.6	0.02	1.8	No	n/a	n/a
6. Simple (<i>giraffe</i>) -S M ₀ P ₀	No	n/a	n/a	n/a	No	n/a	n/a

+/-S marks presence or absence of an onset-embedded stem; +/-M marks whether the stem is related in meaning to the full form; +/-P marks whether the suffix is productive. M₀ and P₀ are used in cases where these descriptions cannot be applied. Relatedness pretest = average pretest scores of semantic relatedness between the whole word and the embedded stem (1-9); freq ratio = ratio of whole word/stem form log frequencies. COALS = corpus-based semantic occurrence metric; Hapax = corpus-based productivity metric (see Methods).

a stronger decompositional hypothesis, the simple presence of a potential stem and a suffix may be sufficient to trigger decompositional processes. Exactly this is seen in the visual domain, where masked priming reveals early decomposition for all derived forms that meet the stem + affix criterion, irrespective of transparency or productivity (Whiting, Shtryov, & Marslen-Wilson, under review; Marslen-Wilson et al., 2008; Rastle et al., 2000). This also holds for regular inflectional morphology in the auditory domain, where the presence of phonological cues to a potential past tense inflection generates L peri-sylvian activation not only for real inflected forms, such as *played*, but also for pseudoregular forms like *trade* or *blend* (Bozic et al., 2010; Tyler et al., 2005). If this holds for the derivational morphology, then the four morphologically complex conditions should all show selective left frontotemporal effects. This should contrast with morphologically simple words like *scandal*, which have an embedded stem (*scan*) but no derivational suffix, or like *giraffe*, which have neither an embedded stem nor a suffix. Both of these sets should engage the bilateral system without selective left inferior frontal gyrus (LIFG) activation.

Whole-form Representations and Perceptual Competition

On a whole-form account of the representation of derived words in English—of which there are historically many versions, from Butterworth (1983) to Baayen et al. (2011)—these forms are neither stored nor accessed as sets of separate morphemes. For spoken language, this means that lexical access requires the sequential mapping of the incoming input onto stored full form representations, without an intervening process that breaks up the string into component morphemes. In this respect, derived stems like *darkness* will engage the same processing mechanisms as morphologically simple stems like *house*, which do not require preliminary parsing.

This makes two predictions for our six experimental conditions. The first is that all stimulus types, from the transparent/productive *bravely* set to the morphologically simple *giraffe* set, will engage the bilateral system and in particular the posterior and middle temporal regions that support stem-based access. No stimulus types should selectively engage the left frontotemporal system (LIFG and STG/MTG) because none of them should trigger decompositional processing. The second prediction is that the relevant processing variables for these word forms will not be their linguistic properties—whether they have a productive suffix or not (+/−P)—but rather their perceptual processing complexity. Perceptual complexity is increased by the presence of a competing onset-embedded stem (+/−S), common to all derived and pseudo-derived forms, as well as to monomorphemic forms like *scandal*. Earlier studies show that the degree of perceptual competition can be captured by the relative frequency of the embedded stem and the whole form (Bozic et al., 2010),

with stronger competition likely to engage bilateral IFG (Zhuang, Tyler, Randall, Stamatakis, & Marslen-Wilson, 2012). The degree of semantic relatedness between the full form and the onset-embedded stem—indexed here as semantic transparency (+/−M)—could also be expected to modulate the competition between the two forms (Raposo, Moss, Stamatakis, & Tyler, 2006).

Data were analyzed using both conventional univariate approaches and multivariate Representational Similarity Analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008). The two methods provide complementary information. Univariate methods allow us to identify how the overall amount of activation per condition maps onto the language processing network and its two systems, with the activation in each condition reflecting the composite influences of linguistic, semantic, and perceptual variables. Multivariate methods such as RSA are sensitive to the informational patterning of neural activity, allowing us to break down these overall effects and obtain specific data about the role of different linguistic, semantic, and perceptual dimensions in the processing of simple and complex spoken forms.

METHODS

Participants

Eighteen right-handed (11 women) native speakers of British English, screened for neurological or developmental disorders, participated in the study. All gave informed consent and were paid for their participation. The study was approved by the Peterborough and Fenland Ethical Committee.

Stimuli

There were six conditions with 40 words each (Table 1). Conditions 1–4 covaried linguistic and semantic variables that are likely to affect morphological decomposability. Conditions 5 and 6 provided morphologically simple control conditions. Condition 5 was made up of words with an embedded pseudo-stem (e.g., *scandal*) but no derivational suffix, and Condition 6 of words with neither pseudostem nor suffix (e.g., *giraffe*).

Linguistic cues to decompositionality were based on suffix productivity. This was initially determined following Ford et al. (2010), Hay and Plag (2004), Bauer (1983), and Marchand (1969). To derive corpus-based values for suffix productivity, we followed the formula used by Ford et al. (2010) and Baayen and Lieber (1991). The probability p that a suffix will be used to create new words is defined as $p = b/N$, where b is the number of *hapax legomena* (words with a given suffix that occur only once in the corpus) and N is the total number of tokens for that affix. This measure reflects the readiness with which a suffix enters into new combinations and is thought to reflect its synchronic productivity.

Semantic, stem-based aspects of decompositionality were captured by manipulating the semantic transparency of the relationship between the embedded stem and the derived full form. Transparency was initially determined by pretests, where participants rated word pairs on a 9-point scale, with 1 being *not related at all in meaning* and 9 being *very related*. Semantically unrelated pairs were rated between 1 and 3, whereas related pairs were rated between 6 and 9. We also used a less subjective corpus-based distance metric based on co-occurrence measures. The semantic relatedness between the derived word and its embedded stem (e.g., *bravely* and *brave*) was estimated using COALS co-occurrence statistics. This is a vector-space method for deriving word meanings (Rohde, Gonnerman, & Plaut, 2005), where a large corpus of text is used to derive the statistics of word co-occurrence, which are expressed as high-dimensional semantic vectors. The pairwise correlations between these vectors provide information about the degree to which the meaning of the embedded stem is preserved in the derived form.

To estimate the perceptual competition between the embedded stem and the whole form during lexical access, we calculated the ratio of the log frequencies of the whole form and the embedded stem. The average value of perceptual competition did not differ significantly across Conditions 1–5 ($p = .12$).

All words and their embedded stems (where present) were matched on word frequency (WF) and lemma frequency (LF), syllable number (SN), and sound file length (SFL) [all $ps > .1$; average condition values in the order *bravely*, *warmth*, *archer*, *breadth*, *scandal*, *giraffe*: log WF = 0.65, 0.52, 0.59, 0.54, 0.70, 0.67; log LF = 0.64, 0.51, 0.57, 0.54, 0.67, 0.65; log stem WF = 1.07, 1.13, 0.95, 0.88, 0.95, n/a; log stem LF = 1, 1.08, 0.91, 0.86, 0.91, n/a; SN = 2.13, 2.18, 2.10, 2.10, 2.13, 2.10; SFL msec = 678, 679, 675, 694, 678, 650]. Each condition contained a mix of grammatical word categories. The 240 test words were mixed with 80 filler words, 240 acoustic baseline trials, and 160 silence trials.

The acoustic baseline trials were constructed to share the complex auditory properties of speech without triggering phonetic interpretation. Musical rain (MuR) achieves this by extracting temporal energy envelopes for each of the speech tokens, which are then filled by jittered fragments of synthesized speech (Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006). The resulting envelope-shaped MuR stimuli are matched in RMS level and long-term spectrotemporal distribution of energy to the corresponding speech stimuli while triggering no speech percept. Fourier transforms and spectrographic analyses of the speech tokens and their corresponding MuR tokens show that their spectra are well matched (Bozic et al., 2010).

Procedure

To maintain the close parallel with our earlier study of inflectional processing (Bozic et al., 2010), we used the

same gap detection task. This is a nonlinguistic task that engages lexical processing (Gaskell & Dumay, 2003; Mattys & Clark, 2002) while keeping task requirements constant across speech and nonspeech stimuli. Short silent gaps (400 msec) were inserted in approximately 20% of trials (60 filler words and 60 MuR trials), and participants were asked to decide as quickly and accurately as possible whether or not words and MuR sounds contained a silent gap. Participants responded using a button box. Only gap-absent trials were subsequently analyzed.

The words were recorded in a sound-proof room by a female native speaker of British English onto a DAT recorder. They were then digitized at a sampling rate of 22 kHz with 16 bit conversion and stored as separate files using CoolEdit. CoolEdit was also used for gap insertion. Items were presented using in-house software, and participants heard the stimuli binaurally over Etymotic R-30 plastic tube phones. Sounds were preemphasized to compensate for distortions imposed by the tube phone presentation.

There were a total of 720 trials, which were pseudo-randomized with respect to their type (test, filler, baseline, null) and presence or absence of gaps, and presented in four blocks of 180 items each. There were five items at the beginning of each block to allow the signal to reach equilibrium. The experiment started with a short practice outside the scanner, where participants were given feedback on their performance. Participants were asked to keep their eyes closed during scanning.

Scanning was performed on a 3T Trio Siemens Scanner at the MRC-CBU, Cambridge, using a fast sparse imaging protocol. Each trial consisted of a 1.4-sec silent period and a 2-sec acquisition, with sounds played within the silent periods to minimize the interference of scanner noise with auditory processing (gradient-echo EPI sequence, repetition time = 3.4 sec, acquisition time (TA) = 2 sec, echo time = 30 msec, flip angle = 78°, matrix size = 64 × 64, field of view = 192 × 192 mm, 32 oblique slices 3 mm thick, 0.75 mm gap). MPRAGE T1-weighted scans were acquired for anatomical localization.

For both univariate and multivariate analyses, preprocessing was performed in SPM5 using the automatic analysis library (github.com/rhodricusack/automaticanalysis). For the univariate analyses, preprocessing involved image realignment to correct for movement, segmentation, and spatial normalization of functional images to the MNI reference brain and smoothing with a 10-mm isotropic Gaussian kernel. The data for each subject were then analyzed using the general linear model, with four blocks and 11 event types (six test conditions, fillers, MuR, fillers with gap, MuR with gap, silence). Motion regressors were included as covariates of no interest to account for any residual movement artifacts. A high-pass filter with a 200-sec cutoff was applied to remove low-frequency noise. The BOLD response for each event was modeled with the canonical HRF and its derivatives. Contrast images were combined into a group random effects analysis. At the group level,

effects across conditions were tested in a repeated measures ANOVA, implemented as a flexible factorial analysis with the six test conditions and subject-specific effects to remove the between subject variability. Differential effects across conditions were tested by F -test effects of interest, followed up by a series of t tests. The reported results are significant at FDR $p < .05$ level, corrected for multiple comparisons.

For the multivariate RSA, general linear models were constructed using unsmoothed native space images that had been realigned and coregistered to the subject's MPRAGE. Data were then extracted for each participant individually using a "sphere of information" searchlight approach (Kriegeskorte, Goebel, & Bandettini, 2006). Here, a roaming spherical spotlight with a standard 5-mm radius (Kriegeskorte et al., 2006) was moved through the gray matter volume, centering onto each voxel in turn and creating a continuous map of local activation patterns. The signal from all voxels in a spotlight is combined to show how well that pattern differentiates between the experimental conditions and therefore reveals the information contained in the pattern. For any given location, this information can be expressed as a representational dissimilarity matrix (RDM), which shows the correlation ($1 - r$ Pearson correlation) between activation elicited by different conditions across voxels. Finally, we tested whether these *data* RDMs correlate with theoretical models, expressed as *model* RDMs, which are generated to test the role of linguistic, semantic, and perceptual variables (see Results for details). This yielded maps of r values for each participant and each model, which were normalized onto the MNI template and statistically evaluated in a second-level analysis using random effects statistics in SPM.

RESULTS

Behavioral Results

All errors (incorrect gap identifications, 1.5%) and time-outs (RT > 3000 msec, 0.1%) were removed, and data were inverse transformed (Ratcliff, 1993). An ANCOVA on the inverse transformed RTs with Condition as a fixed factor and Speech File Duration as a covariate showed significant differences between conditions by subjects, but not by items [$F(5, 85) = 6.38, p < .01$; $F(5, 233) = 1.43, p > .1$]. There were no statistically significant differences in error rates [$F(1, 85) = .63, p > .1$, $F(5, 233) = .80, p > .1$].

Imaging Results

On the basis of previous research (Bozic et al., 2010; Tyler & Marslen-Wilson, 2008; Beeman, 2005; Binder et al., 1997, 2000) and our predictions, we selected bilateral frontotemporoparietal regions as the volume of interest for the analyses. Using WFU Pickatlas, a mask was constructed, consisting of bilateral temporal lobes

(superior, middle, and inferior temporal gyri and angular gyrus), IFG (pars orbitalis, pars opercularis, pars triangularis, precentral gyrus) and the anterior cingulate.

Univariate Analyses

Using classic univariate analyses, we first established the network that supports lower-level acoustic processing. Subtracting null events from the MuR baseline showed strong bilateral activity in Heschl's gyrus and surrounding superior temporal regions (BA 41/BA 42, BA 22, peaks at $-52 -26 2$ and $52 -26 8$), consistent with results from the literature (Uppenkamp et al., 2006; Davis & Johnsrude, 2003; Binder et al., 1997, 2000). This activity is shown in red in Figure 1. To extract the activity specifically related to lexical processes, we contrasted all words with the MuR baseline. This comparison showed that lexical processes activated regions anterior and ventro-lateral to the activity observed for lower-level auditory processing, primarily in bilateral middle, superior, and inferior temporal gyri (BA 21, BA 22, BA 38), spreading to left IFG (BA 45/BA 47), left angular gyrus (BA 39), bilateral fusiform gyrus (BA 37), and anterior cingulate (BA 32; Figure 1, shown in green and Table 2).

Next we focused on the processing of derivational complexity in the frontotemporal network, performing a repeated-measures ANOVA with added subject-specific effects to compare lexical processing (words minus MuR baseline) across the six conditions. This analysis revealed significant differential activation in bilateral middle temporal gyrus (MTG) and in RIFG (Figure 2 and Table 3A). Signal intensity plots for each condition show that all three clusters exhibit a similar activation pattern, where the semantically transparent words with productive suffixes (*bravely*) pattern with simple words (*giraffe*) to produce less activation than either semantically opaque words (*archer*, *breadth*) or semantically transparent words with nonproductive suffixes (*warmth*). No significant differences between conditions emerged in the left inferior frontal areas. When we examined LIFG activations at a lower threshold (see inset signal plot for LIFG in Figure 2), we saw the same pattern as seen for RIFG and for MTG bilaterally. There was no evidence for selective

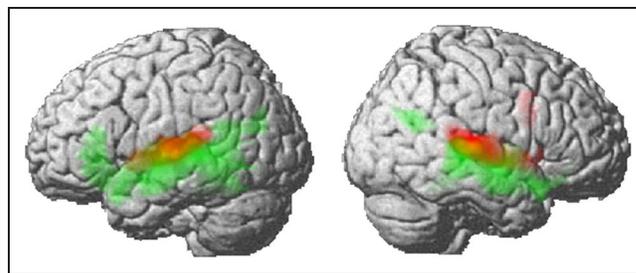


Figure 1. Activation for complex acoustic processing (red) and lexical processing (green) rendered onto the surface of a canonical brain. All results are significant at FDR $p < .05$.

Table 2. Regions Supporting Speech-driven Lexical Processing

Regions	Cluster Extent	Voxel Z	Coordinates		
			x	y	z
<i>Words – MR</i>					
R superior temporal gyrus (BA 22)	3939	6.29	62	0	-2
R MTG (BA 21)		5.57	60	-4	-20
RIFG (BA 47)		5.37	36	24	-20
L MTG (BA 21)	7721	6.04	-54	-12	-6
L MTG (BA 21)		5.92	-64	-34	4
L MTG (BA 21)		5.52	-58	-26	-2
L inferior temporal gyrus (BA 37)*		5.07	-48	-60	-14
LIFG (BA 45)*		4.92	-46	34	0
L angular gyrus (BA 39)*		3.88	-48	-68	16
R parahippocampal region	285	5.00	30	-26	-14
R fusiform		4.49	36	-36	-16
R hippocampus		4.39	26	-18	-12
Anterior cingulate (BA 32)	340	4.34	-6	32	-10
Anterior cingulate (BA 32)		4.14	12	34	-8
Medial frontal area (BA 10)		3.66	2	58	2
R MTG (BA 21)	497	4.11	50	-60	20

All results are significant at FDR $p < .05$ threshold. The three most significant peaks for each cluster are shown. The left temporal cluster also extends into inferior frontal, angular, and inferior temporal areas. The most significant peaks in these regions are marked with an asterisk.

activation of the LH network, even for the highly compositional *bravely* condition. Instead, the *bravely* forms seem to elicit lower levels of activation than the other complex forms, uniformly across the brain.

We further explored this pattern of results in a series of post hoc t tests between individual conditions. Compared with simple words (*giraffe*, $-S M_0 P_0$), all conditions with embedded stems or pseudostems (+S), apart from the

Figure 2. Univariate results showing areas differentially activated by the six conditions, tested by a repeated-measures ANOVA. All results are significant at FDR $p < .05$. Signal plots from the peak voxels of the three clusters show a comparable inverted U-shaped pattern across conditions (the curve shows the global average over clusters). The additional analysis for LIFG (at a lower threshold) is shown as an inset at top left.

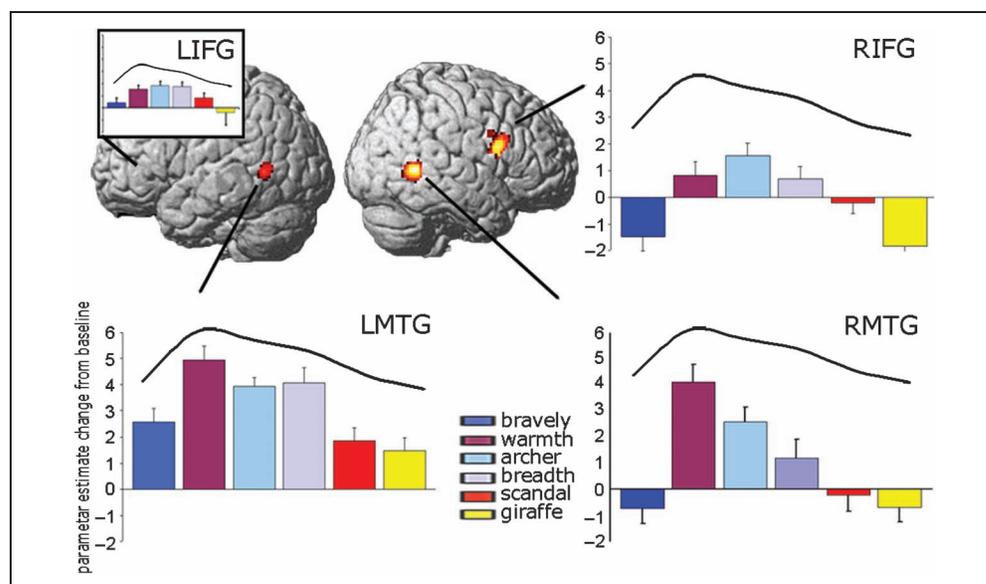


Table 3. Brain Areas Differentially Activated by the Six Conditions, Revealed by a Repeated Measures ANOVA Follow-up Comparisons between Complex and Simple Forms

Regions	Cluster Extent	Voxel Z	Coordinates		
			x	y	z
<i>(A) Brain Areas Differentially Activated by the Six Conditions</i>					
R MTG (BA 21)	229	4.73	58	-54	2
RIFG (BA 44)	252	4.01	60	14	22
RIFG (BA 44)		3.69	50	8	16
R precentral (BA 6)		3.41	52	4	30
L MTG (BA 21)	83	3.57	-52	-56	2
<i>(B) Complex Forms (Warmth, Archer, Breadth, Scandal) vs. Simple Forms (Giraffe)</i>					
RIFG (BA 44)	388	4.23	56	10	18
LIFG (BA 44/6)	82	4.08	-58	8	20
R MTG (BA 21/22)	97	3.68	58	-38	14
R superior temporal gyrus (BA 22)		3.26	62	-32	20
L superior temporal gyrus (BA 22)	78	3.42	-44	-28	8
L MTG (BA 21)	63	3.40	-54	-50	4

All results are significant at FDR $p < .05$.

transparent productive condition (*bravely*, +S +M +P), showed a consistent pattern of increased activation in bilateral frontotemporal regions. Because not all of the clusters from these individual t tests reached statistical significance (due to the limited power of t tests between individual conditions), we grouped the relevant +S conditions together and report the results of this combined analysis (Table 3B). This comparison picks up significant effects in the LIFG as well as in RIFG and bilateral temporal regions, suggesting that the processing of onset-embedded forms is indeed handled by a bilaterally distributed system.

Multivariate Analyses

Here we explore the information encoded in the patterns of neural activity within the frontotemporal language processing network in order to assess the role of the different linguistic, semantic, and perceptual variables that are diagnostic of the engagement of the two processing systems. The multivariate analyses were conducted using RSA combined with a roaming searchlight algorithm (Su et al., 2010; Kriegeskorte et al., 2008). Using a 5-mm radius spherical searchlight, a continuous voxel-by-voxel map of activation patterns was generated for each condition in each participant. These maps are subjected to a multivariate RSA analysis to reveal the correlations between conditions ($1 - r$ Pearson correlation across voxels). At each searchlight location, these correlations are expressed as RDMs (data RDMs) to show the distances between activa-

tion patterns for each pair of conditions. Figure 3 illustrates the roaming searchlight approach and an example RDM. To make inferences about the processing and representational properties of these data RDMs, they were compared at each location against theoretical models, expressed as model RDMs.

Six theoretical RDM models (see Figure 4) were developed to test hypotheses about the critical processing dimensions underlying the brain's response to the experimental stimuli and to assess the relative contributions of linguistic, semantic, and perceptual variables to these responses. For the "linguistic" model RDM, we calculated

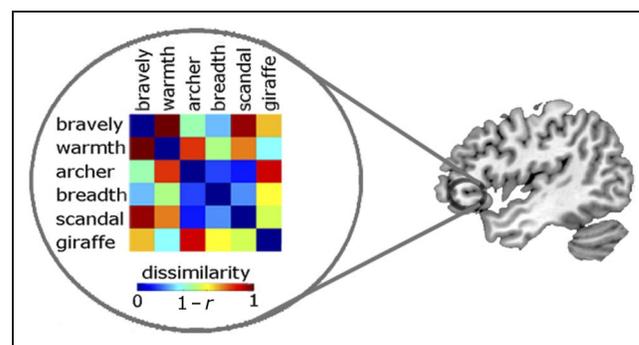
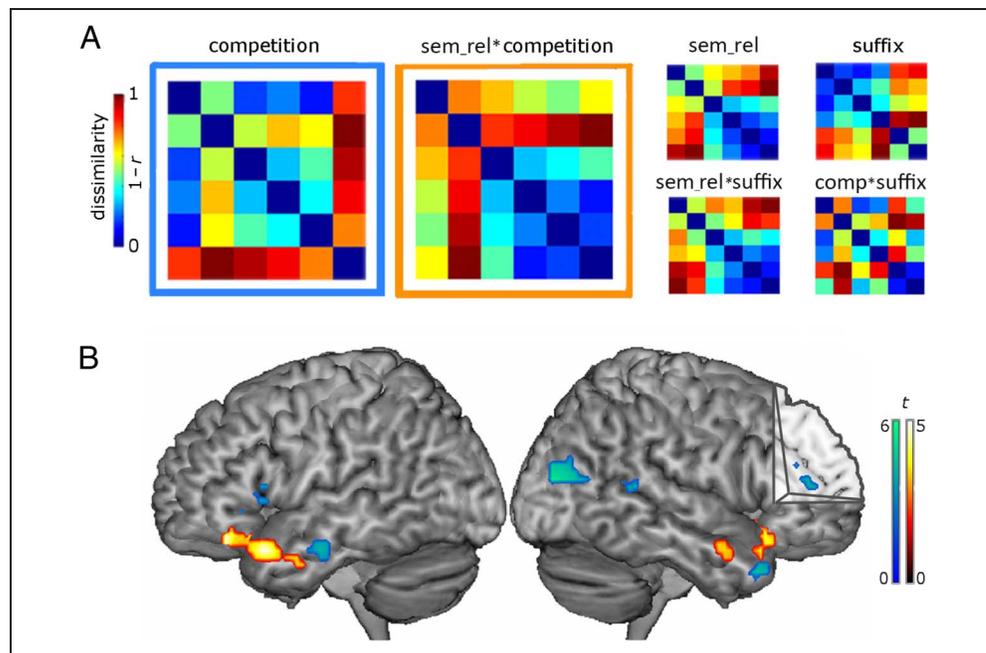


Figure 3. An example RDM extracted at a specific location by the RSA roaming searchlight. The 6×6 matrix reflects the number of experimental conditions and displays the correlation distance ($1 - r$) between the activation patterns for each pair of conditions at a given location.

Figure 4. (A) The six RSA models developed to capture the processing of linguistic, semantic, and perceptual dimensions and their interactions. Only the first two models (perceptual competition and Semantic Relatedness \times Competition interaction) significantly correlated with the activation patterns in the frontotemporal language network. (B) Areas of significant correlation for the competition main effect (blue) and for the Semantic Relatedness \times Competition interaction (orange). All results are significant at FDR $p < .05$.



the productivity for each suffix using the Baayen and Lieber (1991) *bapax legomena* procedure, extracting a quantitative measure of productivity suitable for use in the RSA context. The information whether or not a derivational suffix was present, and whether it was productive or not (+/−P), suffix model, was expected to interact with linguistically specific processes in left-lateralized peri-sylvian areas. To construct the model RDM that tested for effects of semantic transparency (+/−M), *sem_rel*, we used the COALS metric (Rohde et al., 2005), which provides a corpus-based estimate of the semantic relatedness between a word and its embedded stem. To the extent that the semantic transparency of a derived form contributes to its decomposition, the effects were expected to emerge in left-lateralized peri-sylvian areas. If, on the other hand, semantic relatedness between the word and its embedded stem primarily modulates the discriminability of these two competing forms, this variable was expected to engage the bihemispheric system. For the perceptual competition RDM, the estimated degree of competition between a word and its embedded stem (+/−S), *competition* model, was expressed as the ratio of the logged form frequencies of the derived word and the stem (or pseudostem). This model was expected to reflect general perceptual analysis and decision processes in the bihemispheric system. Three further models (Suffix \times Semantic relatedness, Suffix \times Competition, Competition \times Semantic relatedness) were created to test the interactions between these variables.

For each of the continuous variables (suffix productivity, semantic relatedness, perceptual competition, and their respective interactions), we calculated a value for each of the 240 test words (6×40 words per condition).¹ These variables were converted into model RDMs by creating a 240×240 matrix across all the items (one matrix per

variable) and then calculating the average distance between each pair of conditions. This gave us a measure of correlation distances between conditions for each of the variables and their interactions (Figure 4A). The six model RDMs were correlated with the activation RDMs at each location and tested for significance using random effects statistics in SPM. Figure 4B shows maps of significant correlations in the bilateral frontotemporal network.

The results revealed significant bilateral activation for perceptual competition between a word and its embedded stem (+/−S), with the competition model correlating with activation patterns in a distributed set of bilateral temporal areas, left frontal gyrus and bilateral anterior cingulate (AC). A separate cluster of activations in bilateral inferior frontal regions (BA 47) and anterior MTG reflected the interaction of competition with semantic relatedness (*sem_rel* \times competition model). No significant correlations were observed for the linguistically related suffix model (+/−P) or any of its interactions. There was a trend of correlations between the semantic relatedness model and activation patterns in bilateral frontal regions, but these were below threshold. A more detailed listing of the pattern of results is given in Table 4.

DISCUSSION

In the context of more general questions about how the key combinatorial properties of language are handled in the neurocognitive language system, we asked how a major combinatorial language function—derivational word formation—interfaced with the dual language systems we have proposed in earlier research (Bozic et al., 2010; Marslen-Wilson & Tyler, 2007).

Table 4. Regions Significantly Correlated with the Perceptual Competition Model and the Semantic Relatedness \times Competition Interaction

Regions	Cluster Extent	Voxel Z	Coordinates		
			x	y	z
<i>Perceptual Competition Model</i>					
R MTG (BA 21)	22	4.42	48	-42	11
R MTG (BA 21/19)	74	4.17	42	-84	15
R MTG (BA 21/19)		3.71	27	-72	22
R middle temporal pole (BA38)	19	3.72	36	18	-34
L anterior cingulate (BA32)	13	3.63	-3	51	11
L anterior cingulate (BA32)		3.20	-9	39	19
L insula	44	3.60	-42	18	4
LIFG (BA 45)		3.57	-36	27	0
LIFG (BA 44)		3.25	-45	18	11
R anterior cingulate (BA32)	16	3.57	9	33	22
L MTG (BA 21)	27	3.45	-54	-12	-22
L MTG (BA 21)		3.23	-48	-3	-22
<i>Semantics \times Competition Interaction</i>					
RIFG (BA 47)	93	4.32	21	15	-19
RIFG (BA 47)		3.75	39	21	-19
R insula		3.49	30	6	-15
L superior temporal pole (BA 38)	143	4.21	-42	18	-22
LIFG (BA 47)		4.17	-36	36	-15
LIFG (BA 47)		3.70	-24	18	-19
R MTG (BA 21)	22	3.37	48	3	-22

Results are significant at FDR $p < .05$ threshold, corrected for multiple comparisons. Clusters of 12 or more contiguous voxels are reported.

We investigated two sets of hypotheses: If derivationally complex forms are stored and processed with respect to their constituent morphemes, as suggested by decompositional accounts, we expected to observe selective activation of the LH decompositional system, similar to regular inflectional morphology. On a strong decompositional hypothesis, this activation would be seen for all items that contain a stem and a suffix. On a weaker hypothesis, the likelihood of decomposition is modulated by semantic transparency and suffix productivity, so that the strongest selective activation of the LH system is predicted for transparent productive words like *bravely*. On other hand, if derived forms are neither stored nor accessed as sets of separate morphemes, as suggested by whole-form accounts, then we expect no selective engagement of the left frontotemporal system for any of the word sets. Instead, derived words should engage the bilateral system, which supports stem-based, whole-form lexical access. The activation of this system should

primarily reflect the perceptual processing complexity of the words being heard—how easily can they be separated from any competing lexical candidates. We consider first whether or not derived words in English selectively activate the LH decompositional system.

For English regular inflectional morphology, the neural response has two distinctive properties. It is highly left-lateralized, and it contrasts strongly with the bilateral pattern of activation associated with increased nonlinguistic processing demands (Bozic et al., 2010). Testing for these properties in derived words using exactly parallel methods and design and viewing the results from combined univariate and multivariate perspectives, we see no evidence for selective engagement of the LH system. The univariate analyses (Tables 2 and 3 and Figures 1 and 2) show no differential left-lateralized activation associated with the morphologically complex stimuli relative to the other stimulus classes. An ANOVA testing for differential effects across conditions revealed processing differences

in bilateral MTG, as well as right inferior frontal regions. The profile of these differential effects (Figure 2) suggests that they arise from the increased engagement of these regions (as well as LIFG) by the set of perceptually complex but less compositional words (*warmth*, *archer*, *breadth*, *scandal*), compared with more compositional (*bravely*) or simple words (*giraffe*). Strikingly, the *bravely* stimuli seem to pattern throughout with the simple words rather than the complex forms. But there is no evidence that this is because the *bravely* class falls into a distinctively different left-lateralized processing category. Whatever effects are at work here, they seem to apply across the entire bilateral frontotemporal system.

A complementary set of results emerged from the multivariate RSA analyses, which provide a more precise specification of the dimensions that drive the processing of derived words. The RSA searchlight showed that the patterns of voxel activity across frontotemporal regions strongly correlate with levels of perceptual competition (+/−P) and with the modulation of these processes by semantic relatedness (+/−M). These are both dimensions that we associate with the perceptual analysis of whole forms as a function of their cohort competitor environment. No significant correlations emerged for the suffix productivity model (+/−P) nor any of its interactions. Moreover and consistent with the univariate results, the competition-related effects were distributed bilaterally across the regions that support the processing demands associated with mapping from sound to meaning. These analyses suggest that the comprehension of derived words predominantly engages general perceptual processes in the bihemispheric system, rather than specifically linguistic decompositional processes supported by the LH.

Competition and Selection in Bilateral IFG

The two successful RSA models may be capturing, we suggest, two related but separable general purpose processing mechanisms that have been observed across a broad range of stimulus domains and are not restricted to language. The perceptual competition model reflects the simultaneous activation of multiple lexical candidates in words with an embedded stem, which requires additional processing to select the correct candidate. The RSA searchlight shows that this correlates with activity patterns in anterior cingulate, left inferior frontal areas BA 44/BA 45, and bilateral middle temporal regions. Activation in the anterior cingulate has long been associated with competition in general and more specifically with the detection and signaling of the occurrence of conflict in stimulus processing (Botvinick, Cohen, & Carter, 2004; Barch, Braver, Sabb, & Noll, 2000). Similarly, more dorsal IFG (BA 44/BA 45) has been consistently related to selection between automatically retrieved competitors (Zhuang et al., 2012; Zhuang, Randall, Stamatakis, Marslen-Wilson, & Tyler, 2011; Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Thompson-Schill, D’Esposito, & Kan, 1999), often in

the context of a larger network of functionally coupled temporal regions (e.g., Bokde, Tagamets, Friedman, & Horwitz, 2001). In previous research, we have seen a comparable network of activation in the anterior cingulate, left frontal and bilateral temporal regions associated with the detection of increased processing demands in spoken language processing (Stamatakis, Marslen-Wilson, Tyler, & Fletcher, 2005).

In contrast to the perceptual competition model, which seems to be primarily driven by the relative activation strength of an onset-embedded competitor, the Semantics × Competition interaction reflects in addition the semantic distance between the competitors, where greater semantic similarity may affect the discriminability of separate lexemes such as *warm* and *warmth* (Raposo et al., 2006). This model correlated with a more ventral set of bilateral regions, specifically the inferior frontal area BA 47, as well as the temporal pole and anterior MTG. The anterior parts of the IFG have been previously related to lexical semantics (Hagoort, 2005) and to controlled semantic retrieval and the associative strength between words (Badre et al., 2005; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). Several studies have suggested a role for the temporal poles in semantic processing (e.g., Patterson, Nestor, & Rogers, 2007). Competition-related activation in bilateral BA 47 was also observed in our previous study (Bozic et al., 2010), where semantic relatedness between the competitors was not explicitly manipulated, but was significantly correlated with the competition variable. Zhuang et al. (2012) report cohort competition effects in similar ventral IFG regions. In summary, the multivariate RSA analyses not only confirm that the processing of derived words predominantly engages perceptual processes in a bihemispheric system but also allow a more fine-grained specification of the joint but separable variables that underlie this process.

Derivational Morphology in Neurobiological Context

These results have significant implications for an account of the processing and representation of derivationally complex forms in English. First, they contrast strongly with the distinctive left-lateralized decompositional processes seen for English regular inflection. As discussed earlier, both neurocognitive and linguistic properties of regular inflections converge to suggest that they undergo an obligatory decomposition in the recognition process (e.g., Bozic et al., 2010; Bickel & Nichols, 2007; Marslen-Wilson, 2007). Left frontotemporal systems dynamically separate inflected forms into stems, which are the primary carriers of lexical meaning, and into inflectional suffixes, which convey grammatical information but do not interact with the meaning of the stem.

In the current experiment, we saw no selective engagement of the LH system that supports core grammatical computations and no evidence for processing specifically

driven by the properties of derivational suffixes. This is likely to reflect differences in the functional roles of inflectional and derivational morphemes. Unlike inflectional morphemes, derivational morphemes interact with the meaning of the stem they attach to, forming a tight lexicalized connection and creating a new lexical entry in the mental lexicon. These lexical entries vary in their compositionality and predictability, so that the meaning of derived words cannot be reliably computed from the meaning of the stem combined with the meaning of the suffix. Word meaning must instead be represented as a property of the whole form. In such cases, the processing focus will be on the derived form as a whole, and the main processing signatures are likely to reflect the general processing demands associated with separating it from its cohort competitors.

This is a pattern that we expected to see most strongly for the opaque *archer* and *breadth* sets, where the meaning of the whole form was not related to the meaning of the embedded stem or pseudo-stem, and which we also saw for the *warmth* transparent nonproductive set. In all three of these conditions, we saw dominant effects of competition-related variables in the bilateral fronto-temporal system that supports sound-to-meaning mapping for whole-word, stem-based lexical access. In each case, there is likely to be cohort-based competition between the separate lexical entries corresponding to the whole derived form and its embedded stem, with this competition made more complex in the *warmth* case by the semantic similarity between stem and derived form.

This pattern of results across the majority of morphologically complex conditions is consistent with the view that English-derived words are stored as full forms, rather than decompositionally in terms of their component morphemes. However, this cannot be the whole story for two reasons. The first is the results for the *bravely* category. These words, although clearly containing an embedded stem, do not behave as if this generates additional competition-based processing load. The activation profiles in the univariate analysis are much closer to those for the simple words than for complex forms like *warmth*, suggesting a different underlying representation, possibly sensitive to linguistic factors (the synchronic productivity of the suffix) as well as to semantic variables. The second reason is the substantial evidence that semantically compositional words with productive suffixes such as *bravely* or *joyful* robustly facilitate the processing of their stems in overt priming tasks (Longtin, Segui, & Hallé, 2003; Meunier & Segui, 2002; Marslen-Wilson et al., 1994). Overt priming (unlike masked priming) reflects the properties of central lexical representations and suggests that representations for this type of derived word contain a preserved trace of the underlying morphological structure to which the processing system is responsive. Semantic transparency and suffix productivity have also been shown to influence the processing of derived forms in nonpriming studies (e.g., Bertram et al., 2000).

Given this body of evidence, Clahsen et al. (2003) proposed that derivations are stored as separate lexemes, but with preserved marking of morphological structure for semantically transparent forms with productive suffixes (see also Marslen-Wilson, 2007). Such an account may be related to the processing similarity we saw between the transparent productive *bravely* forms and the simple forms like *giraffe*. In the auditory modality—where the input gradually unfolds over time and lexical access requires the sequential mapping of the incoming input onto stored representations—the preserved morphological structure of *bravely* and its conceptual closeness to the competing stem *brave* would make the access to this representation minimally taxing for the comprehension system, similarly to the processing of words that do not have onset-embedded competitors. The presence of morphological marking in the underlying representation of derived forms like *bravely* arguably reflects the linguistic experience of the user, and it is also possible—although not tested here—that it will be influenced by the salience of stem/affix structure in their orthographic input, as there is good evidence that stems and affixes are obligatorily identified in the early stages of visual word recognition (e.g., Marslen-Wilson et al., 2008; Rastle et al., 2000).

In conclusion, the current experiment investigated the processing of English derivational complexity in a neurobiological context. We asked whether derivationally complex words show a similar neurocognitive distribution to regularly inflected words. The results were clear: We saw no selective engagement of the LH systems that support core grammatical computations and no evidence for left-lateralized processes driven by the properties of derivational suffixes. Instead, we observed robust activation in a distributed bihemispheric system, which supports the processing demands associated with mapping from sound to meaning. Responses were primarily driven by the properties of the derived form as a whole, with processing signatures that reflect the demands associated with separating the word from competing alternatives. At the same time, the results for the *bravely* condition suggest that the bilateral system is sensitive to decompositional aspects of lexical representations, with a reduced processing load for semantically and linguistically transparent derived forms. The results have important implications for theories of the processing and representation of English derivational morphology and highlight the fact that the underlying neural substrates provide an essential framework for understanding these processes.

Acknowledgments

This work was supported by a European Research Council Advanced Grant (230570 Neurolex) and Medical Research Council Cognition and Brain Sciences Unit funding to W. D. M.-W. (U.1055.04.002.00001.01). We thank D. Timothy Ives for his help with the musical rain baseline.

Reprint requests should be sent to Dr. Mirjana Bozic or William D. Marslen-Wilson, Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK, or via e-mail: mb383@cam.ac.uk, wdm10@cam.ac.uk.

Note

1. To capture the absence of semantic and competition values for the words without an embedded stem (*giraffe*), a value of 0 was assigned. This was entered into the *sem_rel* and competition models as a constrained normal distribution of random numbers around the mean of 0. The same procedure was applied to nonsuffixed words (*giraffe*, *scandal*) in the suffix.

REFERENCES

- Anderson, S. R. (1992). *A-morphous morphology*. Cambridge: Cambridge University Press.
- Baayen, H., & Lieber, R. (1991). Productivity and English derivation: A corpus-based study. *Linguistics*, 29, 801–844.
- Baayen, R. H., Dijkstra, T., & Schreuder, R. (1997). Singulars and plurals in Dutch: Evidence for a parallel dual-route model. *Journal of Memory and Language*, 36, 94–117.
- Baayen, R. H., Milin, P., Filipovic-Durdevic, D., Hendrix, P., & Marelli, M. (2011). An amorphous model for morphological processing in visual comprehension based on naive discriminative learning. *Psychological Review*, 118, 428–481.
- Badecker, W., & Caramazza, A. (1991). Morphological composition in the lexical output system. *Cognitive Neuropsychology*, 8, 335–321.
- Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, 47, 907–918.
- Barch, D. M., Braver, T. S., Sabb, F. W., & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fMRI study of overt verb generation. *Journal of Cognitive Neuroscience*, 12, 298–309.
- Bauer, L. (1983). *English word formation*. Cambridge: Cambridge University Press.
- Beeman, M. (2005). Bilateral brain processes for comprehending natural language. *Trends in Cognitive Sciences*, 9, 512–518.
- Bertram, R., Schreuder, R., & Baayen, R. H. (2000). The balance of storage and computation in morphological processing: The role of word formation type, affixal homonymy, and productivity. *Journal of Experimental Psychology: Memory, Learning, and Cognition*, 26, 419–511.
- Bickel, B., & Nichols, J. (2007). Inflectional morphology. In T. Shopen (Ed.), *Language typology and syntactic description*, Vol. 3: *Grammatical categories and the lexicon* (pp. 169–240). Cambridge: Cambridge University Press.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S. F., Springer, J. A., & Kaufman, J. N. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, 10, 512–528.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *The Journal of Neuroscience*, 17, 353–362.
- Bokde, A. L. W., Tagamets, M.-A., Friedman, R. B., & Horwitz, B. (2001). Functional interactions of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron*, 30, 609–617.
- Botvinick, M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8, 539–546.
- Bozic, M., Marslen-Wilson, W. D., Stamatakis, E. A., Davis, M. H., & Tyler, L. K. (2007). Differentiating morphology, form, and meaning: Neural correlates of morphological complexity. *Journal of Cognitive Neuroscience*, 19, 1464–1475.
- Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bi-hemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences, U.S.A.*, 107, 17439–17444.
- Butterworth, B. (1983). Lexical representation. In B. Butterworth (Ed.), *Language production* (Vol. 2, pp. 257–294). San Diego, CA: Academic Press.
- Clahsen, H., Sonnenstuhl, I., & Blevins, J. P. (2003). Derivational morphology in the German mental lexicon: A dual mechanism account. In R. H. Baayen & R. Schreuder (Eds.), *Morphological structure in language processing* (pp. 125–155). Berlin: Mouton de Gruyter.
- Davis, M. D., Meunier, F., & Marslen-Wilson, W. D. (2004). Neural responses to morphological, syntactic, and semantic properties of single words: An fMRI study. *Brain and Language*, 89, 439–449.
- Davis, M. H., & Johnsrude, I. S. (2003). Hierarchical processing in spoken language comprehension. *Journal of Neuroscience*, 23, 3423–3431.
- Ford, M. A., Davis, M. H., & Marslen-Wilson, W. (2010). Derivational morphology and base morpheme frequency. *Journal of Memory and Language*, 63, 117–130.
- Friederici, A. D., Ruschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, 13, 170–177.
- Gaskell, G. M., & Dumay, N. (2003). Lexical competition and the acquisition of novel words. *Cognition*, 89, 105–132.
- Goodglass, H., Christiansen, J., & Gallagher, R. (1993). Comparison of morphology and syntax in free narrative and structured tests: Fluent versus nonfluent aphasics. *Cortex*, 29, 377–407.
- Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, 9, 416–423.
- Hamilton, A. C., & Coslett, H. B. (2008). Role of inflectional regularity and semantic transparency in reading morphologically complex words: Evidence from acquired dyslexia. *Neurocase*, 14, 347–368.
- Hay, J., & Plag, I. (2004). What constrains possible suffix combinations? On the interaction of grammatical and processing restrictions in derivational morphology. *Natural Language and Linguistic Theory*, 22, 565–596.
- Hickok, G., Okada, K., Barr, W., Pa, J., Rogalsky, C., Donnelly, K., et al. (2008). Bilateral capacity for speech sound processing in auditory comprehension: Evidence from Wada procedures. *Brain and Language*, 107, 179–184.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8, 393–402.
- Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences, U.S.A.*, 103, 3863–3868.
- Kriegeskorte, N., Mur, M., & Bandettini, P. A. (2008). Representational similarity analysis—Connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, 2, 1–28.
- Leminen, A., Leminen, M., Lehtonen, M., Nevalainen, P., Ylinen, S., Kimppa, L., et al. (2011). Spatiotemporal dynamics of the processing of spoken inflected and derived words: A combined EEG and MEG study. *Frontiers in Human Neuroscience*, 5, 1–14.

- Longtin, C. M., & Meunier, F. (2005). Morphological decomposition in early visual word processing. *Journal of Memory and Language*, *53*, 26–41.
- Longtin, C. M., Segui, J., & Hallé, P. A. (2003). Morphological priming without morphological relationship. *Language and Cognitive Processes*, *18*, 313–334.
- Longworth, C., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (2005). Getting to the meaning of the regular past tense: Evidence from neuropsychology. *Journal of Cognitive Neuroscience*, *17*, 1087–1097.
- Marangolo, P., & Piras, F. (2008). Dissociations in processing derivational morphology: The right basal ganglia involvement. *Neuropsychologia*, *46*, 196–205.
- Marchand, H. (1969). *The categories and types of present-day English word-formation*. Munich: Beck.
- Marslen-Wilson, W. D. (2007). Morphological processes in language comprehension. In G. Gaskell (Ed.), *Oxford handbook of psycholinguistics* (pp. 175–193). Oxford: Oxford University Press.
- Marslen-Wilson, W. D., Bozic, M., & Randall, B. (2008). Early decomposition in visual word recognition: Dissociating morphology, form, and meaning. *Language and Cognitive Processes*, *23*, 394–421.
- Marslen-Wilson, W. D., Hare, M., & Older, L. (1993). Inflectional morphology and phonological regularity in the English mental lexicon. *Proceedings of the 15th Annual Meeting of the Cognitive Science Society*. Princeton, NJ: Erlbaum.
- Marslen-Wilson, W. D., & Tyler, L. K. (1998). Rules, representations, and the English past tense. *Trends in Cognitive Sciences*, *2*, 428–435.
- Marslen-Wilson, W. D., & Tyler, L. K. (2007). Morphology, language and the brain: The decompositional substrate for language comprehension. *Philosophical Transactions of the Royal Society: Biological Sciences*, *362*, 823–836.
- Marslen-Wilson, W. D., Tyler, L. K., Waksler, R., & Older, L. (1994). Morphology and meaning in the English mental lexicon. *Psychological Review*, *101*, 3–33.
- Matthews, P. H. (1991). *Morphology* (2nd ed.). Cambridge: Cambridge University Press.
- Mattys, S. L., & Clark, J. H. (2002). Lexical activity in speech processing: Evidence from pause detection. *Journal of Memory and Language*, *47*, 343–359.
- Meinzer, M., Lahiri, A., Flaisch, T., Hannemann, R., & Eulitz, C. (2009). Opaque for the reader but transparent for the brain: Neural signatures of morphological complexity. *Neuropsychologia*, *47*, 1964–1971.
- Meunier, F., & Segui, J. (2002). Cross-modal morphological priming in French. *Brain and Language*, *83*, 89–102.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*, 976–987.
- Plag, I. (2006). Productivity. In B. Aarts & A. McMahon (Eds.), *The handbook of English linguistics* (pp. 537–556). Oxford: Blackwell.
- Raposo, A., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2006). Repetition suppression and semantic enhancement: An investigation of the neural correlates of priming. *Neuropsychologia*, *44*, 2284–2295.
- Rastle, K., Davis, M. D., Marslen-Wilson, W. D., & Tyler, L. K. (2000). Morphological and semantic effects in visual word recognition: A time-course study. *Language and Cognitive Processes*, *15*, 507–537.
- Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological Bulletin*, *114*, 510–532.
- Rohde, D. L. T., Gonnerman, L., & Plaut, D. C. (2005). *An improved model of semantic similarity based on lexical co-occurrence*. Retrieved from www.cnbc.cmu.edu/~plaut/papers/abstracts/RohdeGonnermanPlautSUB-CogSci.COALS.html.
- Schreuder, R., & Baayen, H. (1995). Modeling morphological processing. In L. Feldman (Ed.), *Morphological aspects of language processing* (pp. 131–154). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Shtyrov, Y., Pihko, E., & Pulvermuller, F. (2005). Determinants of dominance: Is language laterality determined by physical or linguistic features of speech? *Neuroimage*, *27*, 37–47.
- Stamatakis, E. A., Marslen-Wilson, W. D., Tyler, L. K., & Fletcher, P. C. (2005). Cingulate control of frontotemporal integration reflects linguistic demands: A three-way interaction in functional connectivity. *Neuroimage*, *28*, 115–121.
- Su, L., Wingfield, C., Bozic, M., Fonteneau, E., Marslen-Wilson, W. D., & Kriegeskorte, N. (2010). *A multimodal approach to representational similarity analysis*. Poster presented at 16th Annual Meeting of the Organization for Human Brain Mapping.
- Taft, M. (2004). Morphological decomposition and the reverse base frequency effect. *The Quarterly Journal of Experimental Psychology*, *57A*, 745–765.
- Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, *23*, 513–522.
- Tyler, L. K., de Mornay-Davies, P., Anokhina, R., Longworth, C., Randall, B., & Marslen-Wilson, W. D. (2002). Dissociations in processing past tense morphology: Neuropathology and behavioural studies. *Journal of Cognitive Neuroscience*, *14*, 79–94.
- Tyler, L. K., & Marslen-Wilson, W. D. (2008). Frontotemporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *363*, 1037–1054.
- Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., et al. (2011). Left inferior frontal cortex and syntax: Function, structure and behaviour in left-hemisphere damaged patients. *Brain*, *134*, 415–431.
- Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. D. (2005). Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing. *Neuropsychologia*, *43*, 1963–1974.
- Uppenkamp, S., Johnsrude, I. S., Norris, D., Marslen-Wilson, W. D., & Patterson, R. D. (2006). Locating the initial stages of speech-sound processing in human temporal cortex. *Neuroimage*, *31*, 1284–1296.
- Vannest, J., Polk, T. A., & Lewis, R. L. (2005). Dual-route processing of complex words: New fMRI evidence from derivational suffixation. *Cognitive, Affective, and Behavioral Neuroscience*, *5*, 67–76.
- Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*, 329–338.
- Whiting, C., Shtyrov, Y., & Marslen-Wilson, W. D. (under review). Spatiotemporal dynamics of visual word recognition: Morphology, form, and meaning.
- Wright, P., Stamatakis, E. A., & Tyler, L. K. (2012). Differentiating hemispheric contributions to syntax and semantics in patients with left-hemisphere lesions. *Journal of Neuroscience*, *32*, 8149–8157.
- Zhuang, J., Randall, B., Stamatakis, E. A., Marslen-Wilson, W. D., & Tyler, L. K. (2011). The interaction of lexical semantics and cohort competition in spoken word recognition: An fMRI study. *Journal of Cognitive Neuroscience*, *23*, 3778–3790.
- Zhuang, J., Tyler, L. K., Randall, B., Stamatakis, E. A., & Marslen-Wilson, W. D. (2012). Optimally efficient neural systems for processing spoken language. *Cerebral Cortex*, doi:10.1093/cercor/bhs366.