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The role of Broca's area in regular past-tense morphology: An event-related potential study

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Abstract

It has been suggested that damage to anterior regions of the left hemisphere results in a dissociation in the perception and lexical activation of past-tense forms. Specifically, in a lexical-decision task in which past-tense primes immediately precede present-tense targets, such patients demonstrate significant priming for irregular verbs (*spoke-speak*), but, unlike control participants, fail to do so for regular verbs (*looked-look*). Here, this behavioral dissociation was first confirmed in a group of eleven patients with damage to the pars opercularis (BA 44) and pars triangularis (BA 45) of the left inferior frontal gyrus (i.e., Broca's area). Two conditions containing word-onset orthographic-phonological overlap (*bead-bee*, *barge-bar*) demonstrated that the disrupted regular-verb priming was accompanied by, and covaried with, disrupted ortho-phonological priming, regardless of whether prime stimuli contained the regular inflectional rhyme pattern. Further, the dissociation between impaired regular-verb and preserved irregular-verb priming was shown to be continuous rather than categorical; priming for weak-irregular verbs (*spent-spend*) was intermediate in size between that of regular verbs and strong verbs. Such continuous dissociations grounded in ortho-phonological relationships between present- and past-tense forms are predicted by single-system, connectionist approaches to inflectional morphology and not predicted by current dual-system, rule-based models. Event-related potential data demonstrated that N400 priming effects were intact for both regular and irregular verbs, suggesting that the absence of significant regular-verb priming in the response time data did not result from a disruption of lexical access, and may have stemmed instead from post-lexical events such as covert articulation, segmentation strategies, and/or cognitive control.

Keywords

aphasia; Broca's area; left inferior frontal gyrus (LIFG); event-related potentials (ERP); inflectional morphology; regular and irregular past tense

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Introduction

A commonly held view in neuropsychology argues that the non-fluent varieties of aphasia associated with damage to Broca's area result in difficulties with the production and perception of regular past-tense forms, with irregular past-tense forms largely preserved. From the perspective of generative linguistics, this supposed dissociation represents the disruption of a morphological algorithm that (for English speakers) adds or strips the suffix *[-d]*, realized as one of three different allomorphs (*/d/*, */t/*, or */ɪd/*), to or from the present-tense form of regular verbs (e.g., *looked-look*). In contrast, the irregular verbs, which do not fit this pattern (e.g., *spoke-speak*), are represented lexically according to such dual-system perspectives (e.g., Pinker, 1999; Pinker & Ullman, 2002; Marslen-Wilson & Tyler, 1998). A recent dual-system proposal argues that the phonological forms of the regular past tense automatically trigger an attempt at morphological segmentation in any word form containing this "inflectional rhyme pattern" (IRP) (Marslen-Wilson & Tyler, 2007; Marslen-Wilson, 2007; Post et al., 2008). Alternatively, from a connectionist perspective such a dissociation reflects a disruption of phonological processes within a single system that maps the joint phonological and semantic relationships between morphologically related words. Regular past tenses, which overlap heavily with, and share a straightforward mapping to, the corresponding present-tense forms, are more greatly disrupted due to phonological deficits according to such single-system perspectives (e.g., Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003). The nature and robustness of such regular-irregular dissociations following damage to Broca's area is the focus of the current research.

Dissociations in the production of regular and irregular past-tense forms

One way in which regular and irregular past tenses have been argued to dissociate is in overt production tasks. For instance, the participant would be asked to repeat or read a past-tense form, or to generate the past tense from spoken contexts such as "Every day I walk; yesterday I _____." Ullman et al. (1997, 2005) argued that aphasics with anterior/frontal damage, along with people with Parkinson's disease and Huntington's disease, have greater difficulty with regular past-tense forms on these tasks, because of procedural, rule-based deficits. In contrast, they argued that aphasics with posterior/temporal damage, along with people with Alzheimer's disease, have greater difficulty with irregular past-tense forms on these tasks, because of declarative, lexical deficits.

The nature of this dissociation was challenged, however, by Bird et al. (2003, Exps. 1–2), who argued that the deficit in frontal aphasics is not based in morphological rules but rather phonological complexity. They tested a group of ten non-fluent aphasics who showed greater problems with regular verbs on generation tasks and found that the dissociation diminished when the consonant-vowel (CV) structure of the regular and irregular past-tense forms was matched (also see Braber et al., 2005; Lambon Ralph et al., 2005).

Not only has the interpretation of the regular-irregular production dissociation been questioned, it is also unclear whether the dissociation is reliable following frontal lobe damage. Only ten of the fifty non-fluent aphasics screened by Bird et al. (2003) fitted the pattern predicted by Ullman and colleagues. Further, in a meta-analysis of seventy-five non-fluent aphasics, Farooqi-Shah (2007) found no systematic dissociation between regular and irregular verbs on these production tasks. This is consistent with the performance of our patients on production tasks using both the screening and CV-balanced stimuli of Bird and colleagues (Larsen et al., 2008).

Patients with more posterior, fluent forms of aphasia sometimes show irregular past-tense production deficits and preserved performance on regulars (Ullman et al., 1997, 2005). Together, such observations arguably constitute a double dissociation between regular and

irregular past-tense morphology in anterior and posterior aphasics. Whether these deficits in the production of irregular past-tense forms arise from damage to the mental lexicon or instead to semantic processes constitutes a second debate between dual-system and single-system perspectives (Miozzo, 2003; Miozzo & Gordon, 2005; Patterson et al., 2001; Tyler et al., 2004).

The majority of the neuroimaging studies that examined the similarities and differences between regular and irregular morphology also used either overt or covert production of the past tense – and in some cases noun plurals – in English, German, or Spanish (Jaeger et al., 1996; Beretta et al., 2003a; Dhond et al., 2003; Sach et al., 2004; Joanisse & Seidenberg, 2005; Desai et al., 2006; Sahin et al., 2006; de Diego Balaguer et al., 2006; for discussions see Seidenberg & Hoeffner, 1998; Jaeger et al., 1998; Seidenberg & Arnoldussen, 2003; Jaeger, 2003; Beretta et al., 2003b). Like the patient meta-analysis of Faroqi-Shah (2007), these studies also failed to support an anterior-posterior distinction between regular and irregular verb morphology. Generally speaking, the generation of regular and irregular past-tense forms tends to recruit similar cortical networks when compared to reading the corresponding present tense. Further, the majority of these studies demonstrated greater inferior frontal involvement for the production of the *irregular* past, in contrast to the predictions of the declarative-procedural model.

The interpretation of these patterns differed widely among the authors of these studies, with some emphasizing the general similarity of regulars and irregulars (Dhond et al., 2003; Sach et al., 2004; Desai et al., 2006), and attributing the greater activity for irregulars to the single-system notion of less consistent phonological mapping between present- and past-tense form (Seidenberg & Hoeffner, 1998; Seidenberg & Arnoldussen, 2003). Others interpreted any differences between regulars and irregulars as consistent with dual-system approaches (Jaeger et al., 1996; Beretta et al., 2003a; de Diego Balaguer et al., 2006), or focused on the role of the left inferior frontal gyrus (LIFG), arguing for a rule-like grammatical function for this region that would seem to apply equally to both regulars and irregulars (Sahin et al., 2006).

Dissociations in the perception of regular and irregular past-tense forms

The present work follows from a related literature arguing for a dissociation, following damage to the frontal lobe, between regular and irregular past tenses in tasks of perception and lexical access. Marslen-Wilson and Tyler (1997) presented data from a priming task in which past-tense primes immediately preceded present-tense targets, with a lexical decision for the target item. In this study, the two aphasic patients showed priming for irregular items (e.g., *bent-bend*) but inhibition for regular items (e.g., *baked-bake*), whereas controls and a right hemisphere patient showed priming for both. Tyler et al. (2002a, Exp. 1) tested the same two aphasic patients and three additional aphasics in a similar experiment. In this case, the patients as a group demonstrated priming for the irregular items and a flat effect for the regular items, whereas controls primed significantly for both, and primed significantly more for the regular items compared to the patients. Both groups demonstrated significant semantic priming (e.g., *cherry-grape*) but neither demonstrated significant priming for word-onset ortho-phonological overlap (e.g., *gravy-grave*), also known as formal (form-based) priming. In an extension of their work with these patients, Longworth et al. (2005b) found that priming from a past-tense form to a semantically related present-tense form was disrupted for regular pasts (e.g., *blamed-accuse*) but not for irregular pasts (e.g., *shook-tremble*). Marslen-Wilson and Tyler (2007) argued that the lack of priming between regular past-and present-tense forms represents a failure to decompose the morphologically complex regular past tense into stem and affix, resulting in a disruption of lexical access for the corresponding present-tense form.

It is important to note that in studies employing the immediate-priming design, no patient group consistently demonstrates the reverse pattern: preserved priming for regulars and a lack of priming for irregulars. Thus, the single dissociation represented by the lack of regular past-tense priming may simply represent a failure to observe a less robust effect (regular-verb priming) due to the additional variability and statistical noise, whereas a more robust effect (irregular-verb priming) continues to be observed. Indeed, one notable aspect of this experimental design is that in healthy controls, irregular verbs consistently prime numerically, and sometimes significantly, more strongly than regular verbs do (Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a; Tyler et al., 2004; Longworth et al., 2005a; Justus et al., 2008, 2009). This pattern is not to be confused with a different dissociation that is sometimes found when there are intervening items between prime and target. In such delayed-priming designs, it has been argued that only regular pasts prime the corresponding present-tense form (Napps, 1989; Sonnenstuhl et al., 1999; Stanners et al., 1979, but see Fowler et al., 1985; Hanson & Wilkenfeld, 1985).

In the current study, we revisited the dissociation between regular and irregular past-tense priming in anterior aphasics reported by Marslen-Wilson and Tyler (1997) and Tyler et al. (2002a), asking the following four questions.

(1) Does the priming of regular and irregular verbs dissociate following damage to Broca's area?

First, we asked whether this behavioral dissociation – a failure to demonstrate significant priming between regular past-tense forms and present-tense forms, with preserved priming for irregulars – would replicate in a larger, more homogeneous patient group than had been previously reported. We included eleven patients with confirmed damage to Broca's area, operationally defined as the pars opercularis (BA 44) and pars triangularis (BA 45) of the left inferior frontal gyrus (LIFG) (see Keller et al., 2009). Tyler and colleagues (2002a) focused on the role of the LIFG when interpreting the regular-irregular priming dissociation, even though the five patients in that study had extremely diverse left-hemisphere lesions extending far beyond the LIFG into temporal and parietal cortex. A stronger link between disrupted regular-verb priming and damage to the LIFG specifically was shown in a study of 22 brain-lesioned patients who were unselected for lesion location; in this group, tissue density in the LIFG predicted the size of regular-verb priming effects (Tyler et al., 2005a). The present study complements this work by testing regular- and irregular-verb priming in a group of lesion patients who were specifically selected based on damage to the LIFG.

Both dual-system and single-system theories can explain the dissociation between regular- and irregular-verb priming following LIFG damage, but for different reasons. Dual-system approaches (e.g., Pinker 1999; Pinker & Ullman, 2002), including the IRP viewpoint of Marslen-Wilson and Tyler (2007), argue that the LIFG mediates morphological segmentation, whereas the single-system approach (e.g., Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003) argues that the LIFG contributes to phonological processing more generally. Before attempting to distinguish these two interpretations of LIFG function, however, it was essential to confirm that the regular-irregular priming dissociation is in fact associated with damage to this brain region.

(2) Is the regular-irregular dissociation related to phonological factors, and if so, does the inflectional rhyme pattern have special status?

Having documented a dissociation between regular- and irregular-verb priming, we then considered the data in light of competing predictions of the dual-system and single-system approaches. One question that distinguishes the two approaches concerns whether the regular-irregular priming dissociation is related to word-onset ortho-phonological priming.

Two additional priming conditions were included: a pseudopast condition (*bead-bee*), which was designed to mimic the phonological relationship between regular past- and present-tense forms (i.e., the inflectional rhyme pattern or IRP), and an orthophono condition (*barge-bar*), in which prime and target were related by the removal of another phoneme that did not signal a potential morphological relationship. Most dual-system approaches (e.g., Pinker, 1999; Pinker & Ullman, 2002) argue that problems with regular morphology are due to a disruption of rule-based affixation, and do not specifically predict any relationship between regular morphological priming and phonological priming. However, the IRP viewpoint of Marslen-Wilson and Tyler (2007) predicts that regular pseudopast words such as *bead* will be parsed as potential stems and affixes, given that their phonological forms follow the inflectional rhyme pattern of the regular past tense. Thus, the IRP approach predicts that reduced priming for regular verbs should be accompanied by reduced priming for the pseudopast condition alone. The single-system approach (e.g., Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003) argues that problems with regular morphology are based in phonology, but does not explicitly differentiate between different kinds of phonological relationships (such as those that cue morphological relationships and those that do not). Thus, current single-system approaches predict that reduced priming for regular verbs should be accompanied by reduced priming in both the pseudopast and orthophono conditions.

The literature on phonological priming suggests that a combination of pre-lexical facilitation, lexical inhibition, and post-lexical, strategic processes operate simultaneously in designs employing word-onset overlap (McQueen & Sereno, 2005; see Justus et al., 2009, for a review). However, Tyler and colleagues (2002a) did not observe significant phonological priming in controls using the auditory immediate-priming design with lexical decision, making it difficult to evaluate their claims regarding the special status of the inflectional rhyme pattern in this experimental design. Instead, their argument regarding the IRP is based on a different experimental design involving same-different judgments (Tyler et al., 2002b; Tyler et al., 2005b; Post et al., 2008; but see Bird et al., 2003, Exp. 3). However, our group has consistently observed phonological priming in controls with the former design (Justus et al., 2008), allowing for these claims to be tested. One possibility for why Tyler and colleagues did not observe phonological priming is that this condition was underpowered in their stimulus sets (i.e., there were only 24 phonological trials compared to the 48 trials used for morphological conditions; our studies employ 50 items per cell in all conditions). Other relevant factors include inter-stimulus interval (ISI), global relatedness proportions, and the specific stimulus items chosen for the two sets of studies.

(3) Is the regular-irregular dissociation better described as categorical or continuous?

Another question that distinguishes the dual-system and single-system approaches concerns whether the dissociation between regular- and irregular-verb priming reflects a categorical distinction between regular and irregular morphology or a graded continuum of morphological regularity. To address this, the irregular stimuli were separated into two additional categories: *weak irregular verbs*, which are similar to regulars in that they end with a dental stop consonant in the past tense (e.g., *spent-spend*), sometimes by affixation (e.g., *slept-sleep*), and *strong verbs*, which are less similar to regulars, do not involve affixation and instead use a system of vowel changes known as ablaut (e.g., *spoke-speak*). This division allows us to ask whether any regular-irregular dissociation is categorical or continuous. Specifically, if the preserved irregular-verb priming held equally for both kinds of irregularities, this would suggest that the regular-irregular dissociation represents a categorical effect of regularity per se. This would be most consistent with the dual-system approach, which argues that the rule-based regular affixation pattern either is or is not applicable (Pinker & Ullman, 2002). If, however, the preserved irregular-verb priming were

greater for the strong verbs compared to the weak irregular verbs, this would suggest that the regular-irregular dissociation represents a continuous, graded effect (Justus et al., 2008, 2009). Marslen-Wilson and Tyler's (2007) IRP viewpoint, while still positing a categorical division between regular and irregular verbs, might accommodate some degree of continuity in priming effects given that about half of the weak irregular pasts in English contain the inflectional rhyme pattern. Unlike both the traditional dual-system and the IRP approaches, the single-system approach argues that morphological regularity is inherently continuous, and thus specifically predicts that dissociations between regular and irregular verbs will be graded, given that the phonological and semantic differences between the two classes are a matter of degree (see Joanisse & Seidenberg, 1999, 2005; Kielar et al., 2008; Kielar & Joanisse, 2010).

(4) Does the regular-irregular dissociation extend to event-related potentials?

Finally, we asked whether the regular-irregular dissociation could be captured using event-related potentials. In our previous studies using this experimental design, priming between corresponding past-and present-tense forms resulted in reductions of the N400, and in some cases, modulations of the late positive component, or LPC (Justus et al., 2008, 2009). The N400 is a negative-going wave that peaks approximately 400 ms after stimulus onset. The component was first obtained in an experiment in which sentences ended with semantically expected or unexpected words (Kutas & Hillyard, 1980). However, the N400 is also sensitive to word repetition and semantic priming in word pairs (Rugg, 1985) and further can be used to distinguish individual words, in the absence of context, along dimensions such as frequency (Van Petten & Kutas, 1990), neighborhood density (Holcomb et al., 2002), and concreteness (West & Holcomb, 2000). Accordingly, some authors consider the N400 to be an index of lexical access (Lau et al., 2008, 2009) or of the access of conceptual knowledge associated with a word (Kutas & Federmeier, 2000; Van Petten & Luka, 2006; Federmeier, 2007), whereas others consider the component to be an index of post-lexical processes, including semantic integration (Hagoort, 2008).

The neural generators of the N400 component are believed to include large portions of the left temporal lobe, with a smaller contribution from the right, as evidenced by recordings of EEG in patients, intracranial recordings, and magnetoencephalography (Van Petten & Luka, 2006). Therefore, an overall disruption of the N400 component was not expected in the LIFG-defined patient group reported here (see Swick et al., 1998). However, differential modulation of the N400 *effect* (i.e., the degree of difference between the N400s for unprimed and primed items) might be predicted following LIFG damage, just as we might find a change in the relative amount of time it takes to perform lexical decision to primed versus unprimed items, despite no general deficit in the task.

Such a difference would be predicted by the IRP theory of Marslen-Wilson and Tyler (2007) as well as other dual-system theories that posit no whole-word lexical representation for regular past-tense forms, but instead an LIFG-dependent affix-stripping process that detects regular inflections, parses them, and then inputs the stripped present-tense stem to the temporal lobe for lexical access. Within such a framework, LIFG damage would disrupt lexical access for regular past-tense forms. This would be reflected in the ERP data by a reduction in the N400 priming effect for regular verbs. This reduction might be accompanied by a similar reduction for the pseudopast condition, as predicted for the behavioral data.

The single-system perspective makes a similar prediction, but for different reasons. The single-system theory argues that all past-tense forms are fully listed in the lexicon, and that past-tense forms are mapped to the corresponding present tense based on the interacting effects of ortho-phonological and semantic overlap. Accordingly, this approach might

predict that N400 priming effects in this design should reflect the interacting effects of ortho-phonological and semantic priming (see Kiehl & Joanisse, 2010). If damage to the LIFG disrupted priming based on ortho-phonological overlap, and if these effects occurred prior to or during lexical access, then this would also be reflected in the ERP data by a reduction in the N400 priming effect for regular verbs. This reduction might be accompanied by similar reductions for both the pseudopast and orthophono conditions, as predicted for the behavioral data.

The addition of ERP data to the experiment also permits us to examine the events occurring after lexical access, as represented by the N400, but before the participant provides a lexical decision response, often several hundred milliseconds later. The late positive component, or LPC, is a positive going wave beginning at approximately 600 ms after stimulus onset. The component is modulated in some experimental designs by the same lexical-semantic factors that modulate the N400 (Van Petten & Luka, 2006). In others it is modulated by repetition and has been linked to explicit memory processes (e.g., Olichney et al., 2000). Using the current experimental design, we previously observed a modulation of the LPC effect over anterior electrodes in response to word-onset ortho-phonological overlap, which we referred to as a post-lexical anterior negativity or PLAN (Justus et al., 2009). Other authors have reported similar reverse-direction repetition effects, including Holcomb et al. (2005, Exp. 2), who observed it in a study of repetition priming, and Van Petten et al. (2007), who observed it in a study of final-syllable-overlap ortho-phonological priming. We suggested that PLAN modulation of the LPC reflects a relatively late, strategic process driven by word-onset ortho-phonological overlap.

Unlike the N400, there is evidence that neural generators of the LPC include the inferior frontal regions targeted in the current project. Using the Kutas and Hillyard (1980) sentence-context design, Swick and colleagues (1998) showed that patients with damage to inferior frontal regions failed to demonstrate modulation of the LPC by semantic context, suggesting that the main differences between frontal patients and controls lay not in lexical-semantic access, but rather in post-lexical processes beginning around 600 ms following the onset of the critical word. To our knowledge, neither the dual-system theory nor the single-system theory currently acknowledges or makes predictions regarding post-lexical processes in the past-tense priming task, including the contribution of strategies driven by ortho-phonological overlap.

The inclusion of ERP data in the current study as well as other recent work employing immediate morphological priming (Justus et al., 2008, 2009; Kiehl & Joanisse, 2010) complements a larger literature concerning the electrophysiology of morphological processing, which has primarily employed either the delayed-priming design (Weyerts et al., 1996; Münte et al., 1999; Rodríguez-Fornells et al., 2002) or an incorrect-inflection design (Penke et al., 1997; Weyerts et al., 1997; Gross et al., 1998; Rodríguez-Fornells et al., 2001; Morris & Holcomb, 2005; Newman et al., 2007). The current work, in which neuropsychological and ERP methods are combined, also complements the literature concerning the N400 in aphasia (Friederici et al., 1998, 1999; Hagoort et al., 1996; Swaab et al., 1997, 1998).

Method

Participants

To maximize the neural homogeneity of the patient group, we adopted lesion-based rather than symptom-based inclusion criteria for this study. Eleven patients were recruited based on damage to Broca's area, operationally defined as the pars opercularis (BA 44) and pars triangularis (BA 45) of the LIFG, following a single infarction in the precentral branch of

the middle cerebral artery. Lesions were documented by CT or MRI scans and reconstructed onto a standard brain template of the Montréal Neurological Institute using MRICro software (Rorden & Brett, 2000). These lesion reconstructions are presented for every patient in Figure 1, and the extent of damage in the pars opercularis, pars triangularis, pars orbitalis, and the insula is provided in Table 1.

All patients had a history of clinically significant aphasia. However, no specific aphasia diagnosis was required for inclusion in this study. The patients typed as four anomic aphasics, one Broca's aphasic, three unclassifiable aphasics, and three within normal limits (WNL) on the most recent administration of the Western Aphasia Battery (WAB). The subscores of the WAB are also provided in Table 1. Note that, had we adopted the requirement that all patients have a diagnosis of Broca's aphasia, the size and anatomical diversity of the patients' lesions would have increased dramatically, as a chronic Broca's aphasia requires a large lesion encompassing the frontal and anterior temporal cortices, underlying white matter, the insula, and basal ganglia, and which does not necessarily include Broca's area in the LIFG (Dronkers et al., 2007; Dronkers & Baldo, 2009). Therefore, a lesion-based inclusion criterion was the most appropriate for testing the hypothesis that the absence of significant regular-verb priming is specifically associated with damage to the LIFG (Tyler et al., 2002a; Tyler et al., 2005a).

The eleven patients (aged 58 $\pm$ 12 years; education 16 $\pm$ 3 years; 4 women, 7 men) were matched to eleven controls (aged 57 $\pm$ 12 years; education 16 $\pm$ 3 years; 3 women, 8 men). All participants were right-handed and native speakers of US English. All procedures were approved by the institutional review board of the VA Northern California Health Care System, and written informed consent was obtained from all participants.

Procedure

Following the informed consent procedure and application of the recording electrodes, participants were seated in a sound-attenuated booth. Each trial of the experiment began with fixation for 1500 ms, followed by the prime, spoken by a female voice. The target was presented 1400 ms after the onset of the prime (an average of 870 ms ISI, given mean prime length of 530 ms), spoken by a male voice. Participants were instructed to identify quickly and accurately whether the target (male) voice was saying a real word or a nonword. Given that seven of the patients demonstrated some degree of right-sided hemiparesis, all participants were required to respond using the left hand, and were encouraged to use the middle and index fingers to respond to non-words and real words, respectively.

Design and Selection of Stimuli

The 1200 stimulus items of Justus et al. (2008) were used, resulting in 600 prime-target pairs according to a 4 (regular, irregular, pseudopast, orthophono) by 3 (primed, unprimed, nonword) design with 50 trials per cell (Table 2). All cells consisted of 46 monosyllabic prime-target pairs and 4 bisyllabic prime-target pairs. All of the 600 primes and 400 of the 600 targets were real words, selected with the aid of the CELEX Lexical Database (Baayen et al., 1995). The remaining 200 targets were selected using the ARC Nonword Database (Rastle et al., 2002).

One design constraint that was adopted given the use of ERP data (requiring at least 50 items per cell), the desire to avoid repetition effects on the N400 (observed even for extremely long lags; Nagy & Rugg, 1989; Bentin & Peled, 1990), and the small number of available stimuli in some conditions (especially the pseudopast condition) was the decision to use a between-item design. Accordingly, extreme care was taken to balance the items used in the primed and unprimed conditions – as well as the prime words in the nonword

condition – on factors such as lemma frequency, syllabicity, word class, number of phonemes, number of letters, and in the case of irregular verbs, the type of irregularity. This was done simultaneously with the constraint to balance the same factors as closely as possible between the regular, irregular, pseudopast, and orthophono conditions. Further constraints on the selection of stimulus items for each Word Type were as follows.

Regular Verbs—150 regular verbs were selected and divided among the primed, unprimed, and nonword conditions. All were the /t/ or /d/ rather than the /ɪd/ allomorph, in order to control for syllabicity with the other conditions. Regular past tenses that shared pronunciations with other words were avoided (e.g., *packed/pact* or *missed/mist*).

Irregular Verbs—150 of the ~180 irregular English verbs were selected. Modal forms (e.g., *could-can*, *would-will*) were avoided, as were words that are typically regularized in US English (e.g., *learnt-learn*, *spilt-spill*). The chosen items were divided among primed, unprimed, and nonword conditions as follows. First, to avoid repetition priming, the 26 no-change irregulars (e.g., *put*) were used as primes only in the nonword condition. The remaining 45 weak irregulars in the set (e.g., *spent-spend*) were divided between the primed ($n = 23$) and unprimed ($n = 22$) conditions. The rest of the words in the three conditions ($n = 27, 28$, and 24) were strong verbs (e.g., *spoke-speak*), or, in two cases, suppletive verbs (*was-is*, *went-go*). Care was taken to distribute the subordinate families of irregular verbs as evenly as possible throughout the three conditions, given these constraints.

Pseudopast—50 pairs of semantically unrelated words were selected in which the prime word differed from the target word by the addition of /t/ or /d/, in a manner phonologically consistent with the inflectional rhyme pattern of the regular past tense (e.g., *bead-bee*). Potential stimuli overlapping with items in the verb conditions (e.g., *field-feel*, *bide-buy*) or sharing pronunciations with regular verbs of a higher word frequency were avoided. Given the small number of appropriate monosyllabic pairs available in English, these 50 pseudopasts were all used in the primed condition. The items in the unprimed and nonword conditions were designed by choosing items of the same word class, frequency, and, to the extent possible, number of phonemes and letters as in the primed condition.

Orthophono—50 pairs of semantically unrelated words were selected in which the prime word differed from the target word by the addition of a single phoneme and one or two letters (e.g., *barge-bar*). Unlike in the pseudopast condition, this addition was not phonologically consistent with the inflectional rhyme pattern of the regular past tense, and the spelling of the shorter target word was completely contained within the spelling of the longer prime word. These 50 orthophono prime-target pairs were all used in the primed condition. As in the pseudopast condition, the items in the unprimed and nonword conditions were designed by choosing items of the same word class, frequency, and number of phonemes and letters as in the primed condition.

The entire stimulus set may be viewed in the Appendix of Justus et al. (2008).

Stimulus Recording

Sound files were digitally recorded in a sound-attenuated booth by two native speakers of US English, one woman (prime words) and one man (target words), who were naïve to the purpose of the experiment. The speakers were coached in pronouncing the real words and nonwords correctly, and in delivering all items clearly and with a consistent intonation, sound level, and speed. A pseudorandom recording order was created to ensure that no changes in speech over the course of the recording session would correlate with experimental factors.

Recordings were later filtered of white noise, edited into individual sound files, and further normalized for sound level. Analyses of sound file lengths confirmed that these were properly balanced (see Table 2).

EEG Recording

Electroencephalographic (EEG) activity was recorded using 26 electrodes embedded in an electrode cap. These electrodes consisted of the 19 electrodes of the International 10–20 system (Jasper 1958) plus 7 additional electrodes at positions AF3/4, FC5/6, CP5/6, and POz. Four external electrodes recorded the left mastoid, right mastoid, left-horizontal electrooculogram (EOG), and left-vertical EOG. During acquisition, EEG was recorded with reference to the left mastoid. Signals were amplified ($\times 20,000$), filtered (0.1–80 Hz), and digitized at a sampling rate of 256 Hz (SA Instrumentation). Data were later re-referenced to the average of the two mastoids and digitally low-pass filtered (20 Hz). Eye-blinks that were uncontaminated by additional artifacts were corrected using an adaptive filtering algorithm.

Mean amplitudes were calculated relative to a 100-ms window preceding word onset. No main effects of Electrode are reported. Interactions involving Electrode are reported with uncorrected F values and degrees of freedom, and with Greenhouse-Geisser corrected p values.

Topographic maps were created by calculating voltage differences between the unprimed and primed conditions at each electrode and interpolating voltage differences for the rest of the scalp using a spherical spline mapping method (Perrin et al., 1989).

Results

Behavioral Data

The first analyses of the behavioral data address the first two of the four main questions posed by this paper, namely whether the priming of regular and irregular verbs dissociates following damage to Broca's area, and whether this dissociation can be explained in terms of ortho-phonological priming (Figure 2, upper four plots). Behavioral data were first analyzed using four analyses of variance with the factors Word Type (regular, irregular, pseudopast, orthophono) and Priming (primed, unprimed), separating the controls and the patients, for the response time and error rate data. These were followed by additional analyses comparing the degree of Priming for each possible pair of Word Types. A final group of analyses evaluated whether the degree of Priming for each Word Type differed significantly between controls and patients. For the response time analyses, only correct responses to real words were used. Such responses falling beyond the individual mean plus three standard deviations were removed (a mean of 2.2 instances per person for the patients and 3.2 for the controls).

The main effect of Priming was reliable for the controls in both response times and errors [RT: $F(1,10)=28.4$, $p<.001$; errors: $F(1,10)=7.5$, $p=.02$] but for the patients was reliable only in the errors [RT: $F(1,10)=1.7$, $p=.23$; errors: $F(1,10)=16.7$, $p=.002$]. The main effect of Word Type was reliable in both measures for both the controls [RT: $F(3,30)=35.8$, $p<.001$; errors: $F(3,30)=34.4$, $p<.001$] and the patients [RT: $F(3,30)=28.7$, $p<.001$; errors: $F(3,30)=16.5$, $p<.001$]. Finally, the interaction between Priming and Word Type was reliable in response times for the controls [RT: $F(3,30)=7.3$, $p=.001$; errors: $F(3,30)=1.8$, $p=.16$] and in both response times and errors for the patients [RT: $F(3,30)=10.0$, $p<.001$; errors: $F(3,30)=40.6$, $p=.02$].¹

For the controls, significant RT priming was found for regular verbs [RT: 44 ms, $t(10)=4.0$, $p=.002$; errors: 1.1%, $t(10)=2.2$, $p=.05$], irregular verbs [RT: 102 ms, $t(10)=6.0$, $p<.001$;

errors: 0.7%, $t(10)=1.2$, $p=.27$], pseudopast [RT: 40 ms, $t(10)=2.5$, $p=.03$; errors: 2.9%, $t(10)=3.0$, $p=.02$], and orthophono [RT: 32 ms, $t(10)=2.3$, $p=.04$; errors: 1.6%, $t(10)=1.5$, $p=.17$]. Further, greater RT priming was observed for irregular verbs compared to regular verbs [$F(1,10)=29.6$, $p<.001$], irregular verbs compared to pseudopast [$F(1,10)=9.7$, $p=.01$], and irregular verbs compared to orthophono [$F(1,10)=17.4$, $p=.002$]. Greater error priming was observed for the pseudopast compared to irregular verbs [$F(1,10)=5.7$, $p=.04$].

For the patients, significant RT priming was found only for the irregular verbs [98 ms, $t(10)=5.3$, $p<.001$; errors: 2.5%, $t(10)=2.1$, $p=.06$], and not for regular verbs [RT: 5 ms, $t(10)=0.2$, $p=.82$; errors: 1.8%, $t(10)=2.3$, $p=.09$], pseudopast [RT: -23 ms, $t(10)=-0.8$, $p=.43$; errors: 8.2%, $t(10)=3.5$, $p=.006$], or orthophono [RT: -2 ms, $t(10)=0.1$, $p=.89$; errors: 3.6%, $t(10)=2.3$, $p=.04$]. However, error effects or trends were observed for all four Word Types. The lack of a significant regular priming effect is not dependent on the inclusion of P7 (see Figure 2); if P7 were removed from the analysis, the regular RT effect would increase to a trend but remain nonsignificant (20 ms, $t(9)=1.5$, $p=.17$). Further, greater RT priming was observed for irregular verbs compared to regular verbs [$F(1,10)=20.5$, $p=.001$], irregular verbs compared to pseudopast [$F(1,10)=13.3$, $p=.004$], and irregular verbs compared to orthophono [$F(1,10)=18.0$, $p=.002$]. Greater error priming was observed for pseudopast compared to irregular verbs [$F(1,10)=6.2$, $p=.03$] and pseudopast compared to regular verbs [$F(1,10)=8.3$, $p=.02$].

To ascertain whether priming for each Word Type was significantly different between the controls and the patients, the interaction between Priming and Group was examined for each Word Type separately. The interaction did not reach significance for regular verbs [RT: $F(1,20)=2.9$, $p=.10$; errors: $F(1,20)=0.5$, $p=.51$], irregular verbs [RT: $F(1,20)=.04$, $p=.85$; errors: $F(1,20)=1.8$, $p=.20$], pseudopast [RT: $F(1,20)=3.8$, $p=.07$; errors: $F(1,20)=4.3$, $p=.05$], or orthophono [RT: $F(1,20)=2.9$, $p=.11$; errors: $F(1,20)=1.1$, $p=.31$]. However, the trends support the results of the separate analyses that priming was reduced for the patients relative to the controls for regular verbs, pseudopast, and orthophono, and preserved for irregulars.

Correlations Within the Response Time Data—Given that a major interest of this study was to explore the relationship between regular-verb priming and word-onset ortho-phonological priming, one might ask whether the size of the regular priming effect co-varied with that of the pseudopast and orthophono conditions. The relationship between priming effect sizes and mean response time was also of interest. To address this, a series of Pearson correlations was performed on the difference between primed and unprimed RT for each Word Type, along with the mean response time (5 items, 10 pairings), using the Holm-Bonferroni correction. Mean response time (specifically, mean correct response time to all real words) was negatively correlated with the size of the regular [$r(20)=-.68$, $p<.001$], pseudopast [$r(20)=-.76$, $p<.001$], and orthophono [$r(20)=-.62$, $p=.002$] priming effects, but not with the irregular priming effect [$r(20)=-.12$, $p=.60$]. Further, the regular priming effects correlated with the pseudopast [$r(20)=.55$, $p=.008$] and orthophono effects [$r(20)=.55$, $p=.009$], but irregular priming effects did not [each $p>.35$]. Finally, regular and irregular priming effects correlated [$r(20)=.52$, $p=.01$], as did pseudopast and orthophono effects [$r(20)=.48$, $p=.02$]; however, these last correlations do not survive correction for multiple comparisons.

¹The direction of significant main effects of Priming and Word Type were consistent across RTs and errors (i.e., conditions associated with faster RTs had fewer errors). Priming by Word Type interactions tended to be reversed for RTs and errors (i.e., Word Types associated with larger RT priming effects had smaller error priming effects).

Effects of the Type of Irregularity—To address the third main question posed by this paper, namely whether the regular-irregular dissociation observed in the patient group would be better described as categorical or continuous, the data for the irregular verbs were divided into two subsets – weak irregular verbs and strong verbs (Figure 2, lower four plots). Two analyses with the factors Irregular Subset (weak irregular, strong) and Priming (primed, unprimed) tested for an interaction between these variables, followed by sets of two planned comparisons to test for priming in each irregular subset alone. The interaction was significant in the RT data for both the controls [RT: $F(1,10)=32.3$, $p<.001$; errors: $p=.55$] and the patients [RT: $F(1,10)=11.7$, $p=.007$; errors: $p=.14$], such that greater priming was observed for the strong verbs compared to the weak irregular verbs. Both the weak irregular verbs and the strong verbs resulted in significant RT priming when examined separately, for both the controls [weak irregular RT: 58 ms, $t(10)=2.6$, $p=.03$; errors: $p=.19$; strong RT: 162 ms, $t(10)=8.2$, $p<.001$; errors: $p=.72$] and the patients [weak irregular RT: 74 ms, $t(10)=3.8$, $p=.003$; errors: $p=.59$; strong RT: 154 ms, $t(10)=6.1$, $p<.001$; errors: $t(10)=2.3$, $p=.05$], with the patient strong-verb effect also reaching significance for the errors.

To complete the evaluation of the three verb classes, comparisons were made between the regular verbs and each subset of the irregular verbs. Unsurprisingly given the results above, strong verbs resulted in greater RT priming than did the regular verbs, for both the controls [RT: $F(1,10)=50.0$, $p<.001$; errors: $p=.52$] and the patients [RT: $F(1,10)=37.3$, $p<.001$; errors: $p=.19$]. However, the weak irregular verbs primed more strongly than did the regular verbs for just the patients [RT: $F(1,10)=8.5$, $p=.02$; errors: $p=.28$] but not for the controls [RT: $F(1,10)=0.9$, $p=.37$; errors: $p=.83$].

ERP Data

The remainder of the analysis addresses the fourth main question, concerning whether the regular-irregular dissociation extends to event-related potentials. Visual inspection of the averaged waveforms revealed the N400 component, which was centered over central-posterior electrodes. In both groups and for all four word types, the N400 component was numerically less negative for primed trials compared to unprimed trials. Accordingly, a nine-electrode region of interest (Cz, Pz, POz, C3, C4, CP5, CP6, P3, P4) was chosen to examine the relative sizes of the ERP effects across the four conditions (Figure 3).

Following the N400, during the late positive component of the waveform, two effects emerged: in some cases the N400 priming effect was preserved through the LPC (see especially the irregular verbs), whereas for other conditions the waveforms crossed at approximately 600 ms, such that the LPC was more negative for primed trials than for unprimed trials (see especially the pseudopast). Given these observations, two temporal windows were chosen for the analysis – an early window of 350–600 ms, to examine the N400 component, and a late window of 600–850 ms, to examine the LPC (Figure 4). These analysis windows were slightly delayed and elongated relative to those used in our previous intra-modal study of healthy young controls (300–500 and 500–700 ms), consistent with previous work concerning the N400 component in normal aging (Federmeier & Kutas, 2005) and in aphasia (Hagoort et al., 1996; Swaab et al., 1997).

ERP data were first analyzed using four analyses of variance with the factors Word Type (regular, irregular, pseudopast, orthophono), Priming (primed, unprimed), and Electrode (9-electrode ROI), separating the controls and the patients, as well as the N400 (350–600 ms) and LPC (600–850 ms) windows. These were followed by additional follow-up analyses to compare the relative sizes of the various priming effects, and whether they differed significantly between controls and patients, in a manner parallel to the response time and error analyses.

N400 Window (350–600 ms)—For the controls during the N400 window, main effects of Priming [$F(1,10)=9.0, p=.01$] and Word Type [$F(3,30)=4.2, p=.01$] were reliable, as well as an interaction trend between these variables [$F(3,30)=2.4, p=.08$]. When considering the four Word Types individually, reliable N400 priming effects were observed for regular verbs [$F(1,10)=4.9, p=.05$] and irregular verbs [$F(1,10)=29.9, p<.001$]. A marginal effect was observed for the pseudopast condition [$F(1,10)=4.2, p=.07$], whereas no effect was observed for the orthophono condition [$F(1,10)=0.6, p=.46$]. The N400 reduction for primed irregular verbs was significantly larger than that for pseudopast [$F(1,10)=6.0, p=.03$] and marginally larger than that for orthophono [$F(1,10)=3.8, p=.08$]. The other four pairings were not significant ($p>.20$).

For the patients during the N400 window, main effects of Priming [$F(1,10)=23.1, p=.001$] and Word Type [$F(3,30)=3.1, p=.04$] were reliable. The interaction between Priming and Word Type was not ($p=.99$). When considering the four Word Types individually, reliable or marginal N400 priming effects were observed for both regular verbs [$F(1,10)=8.8, p=.01$] and irregular verbs [$F(1,10)=3.7, p=.08$], and further, for the pseudopast [$F(1,10)=10.2, p=.01$] and orthophono [$F(1,10)=18.5, p=.002$] conditions. None of these N400 reductions were significantly larger than the others (six pairings, each $p>.70$).

To determine whether the N400 priming effect for each Word Type was significantly different between the controls and the patients, the interaction between Priming and Group was examined for each Word Type separately. The interaction was not significant for regular verbs [$F(1,20)=0.4, p=.51$], irregular verbs [$F(1,20)=.001, p=.98$], pseudopast [$F(1,20)=2.1, p=.16$], or orthophono [$F(1,20)=1.9, p=.19$].

LPC Window (600–850 ms)—For the controls during the LPC window, the main effect of Word Type [$F(3,30)=8.1, p<.001$] and the interaction between Priming and Word Type were reliable [$F(3,30)=5.7, p=.003$]. The main effect of priming was not ($p=.80$). When considering the four Word Types individually, significant priming was observed for irregular verbs [$F(1,10)=6.9, p=.03$], in the same direction as the N400 priming effect. A marginal reversed effect was observed for the pseudopast condition [$F(1,10)=4.6, p=.06$], such that primed items were more negative than unprimed items. Neither the regular ($p=.72$) nor the orthophono ($p=.27$) effect was significant during this later window. Considering the Word Types in pairs, the irregular effect was significantly different from both the pseudopast [$F(1,10)=14.2, p=.004$] and orthophono [$F(1,10)=11.3, p=.007$] effects. The regular effect trended towards a difference from pseudopast [$F(1,10)=3.2, p=.10$] and orthophono [$F(1,10)=3.9, p=.08$]. The other two pairings were not significant ($p>.18$).

For the patients during the LPC window, main effects of Priming [$F(1,10)=7.8, p=.02$] and Word Type [$F(3,30)=5.0, p=.006$] were reliable. The interaction between Priming and Word Type was not ($p=.17$). When considering the four Word Types individually, significant priming was observed for irregular verbs [$F(1,10)=7.6, p=.02$] and orthophono [$F(1,10)=5.8, p=.04$], both in the same direction as the N400 priming effect. The effect for regular verbs was not significant during this later window [$F(1,10)=1.5, p=.25$], nor was the effect for pseudopast [$F(1,10)=0.9, p=.37$], despite this condition showing a numerically reversed effect as in the controls. Consistent with this observation, the pseudopast effect trended towards a difference from both the irregular [$F(1,10)=4.3, p=.07$] and orthophono [$F(1,10)=3.5, p=.09$] effects. The other four pairings were not significant ($p>.20$).

To determine whether the LPC priming effect for each word type was significantly different between the controls and the patients, the interaction between Priming and Group was examined for each Word Type separately. The interaction was not significant for regular

verbs [$F(1,20)=0.6, p=.44$], irregular verbs [$F(1,20)=0.5, p=.47$], or pseudopast [$F(1,20)=0.4, p=.51$], and just reached significance for orthophono [$F(1,20)=4.4, p=.05$].

Effects of the Type of Irregularity—Potential effects of the type of irregularity within the irregular word set on the N400 and LPC were explored using analyses of variance with the factors Irregular Subset (weak irregular, strong), Priming (primed, unprimed), and Electrode (9-electrode ROI), specifically to examine for an interaction between Irregular Subset and Priming. Unlike in the behavioral data, this interaction was not significant during the N400 window for either the controls ($p=.12$) or the patients ($p=.61$), nor was it significant during the LPC window for either the controls ($p=.72$) or the patients ($p=.93$).

Correlations Within the ERP Data—As before, one might ask whether the size of the N400 priming effect for regular verbs co-varied with that of the pseudopast and orthophono conditions. A series of Pearson correlations was performed on the average difference in the nine-electrode ROI for each Word Type during the N400 and LPC windows (8 items, 28 pairings), using the Holm-Bonferroni correction. The N400 priming effects for the pseudopast and orthophono conditions correlated [$r(20)=.64, p=.002$], but these effects did not correlate with the N400 priming effect for regular verbs (each $p>.40$). Further, the N400 priming effect for each Word Type correlated with the corresponding LPC effect (each $p<.002$).

Correlations Between the Response Time and ERP Data—Given the relationships found between regular, pseudopast, and orthophono priming effects in the behavioral data, and the lack of such relationships in the N400 data, one might ask whether the size of the behavioral priming effects predicted the size of the N400 priming effects, either for the corresponding condition or between conditions. A series of Pearson correlations was performed to compare the mean response time to all real words, the four RT difference scores for each Word Type, and the eight ERP difference scores (40 pairings). None of these correlations were significant after the Holm-Bonferroni correction was applied.

Lesion and Western Aphasia Battery Data

A final analysis was carried out to determine whether the lesion extent in our region of interest, LIFG pars opercularis (BA 44) and pars triangularis (BA 45), predicted the size of the behavioral or ERP priming effects. To explore the lesion variability outside of Broca's area, ten other brain regions that were implicated in some members of the current patient group were included in this analysis: LIFG pars orbitalis, insula, middle frontal gyrus, rolandic operculum, putamen, precentral gyrus, postcentral gyrus, superior temporal pole, superior temporal gyrus, and Heschl's gyrus. Similarly, the four subscores of the Western Aphasia Battery (fluency, comprehension, repetition, and naming), which are used to determine WAB aphasia type, were entered into this analysis. Only one correlation survived correction for multiple comparisons: lesions affecting a greater percentage of the insula were associated with smaller ERP priming effects for the irregular verbs in the N400 window [$r(9)=.93, p<.001$]. None of the correlations between a behavioral priming score and either lesion or WAB data approached significance, even when uncorrected for multiple comparisons. Note that because the patients were selected for a relatively high degree of lesion uniformity (i.e., all affecting the pars opercularis and pars triangularis), as opposed to the unselected patient population that might be used in a true lesion-symptom mapping analysis (e.g., Bates et al., 2003; Tyler et al., 2005a), correlations implicating these two regions were not expected.

Discussion

The present study first confirmed previous observations (Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a; Tyler et al., 2004; Longworth et al., 2005a; Justus et al., 2008, 2009) that, in neurologically healthy people, hearing the past-tense form of both regular and irregular English verbs facilitated an auditory lexical decision to the corresponding present-tense form (e.g., *looked-look*, *spoke-speak*). This behavioral facilitation was accompanied by a reduction in the N400 component to the target word. Here we tested eleven patients with damage to Broca's area, i.e., the LIFG pars opercularis (BA 44) and pars triangularis (BA 45), along with eleven matched controls, to see whether a previously observed behavioral dissociation between regular and irregular morphological priming (Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a) would replicate in this well-defined patient group. Second, we asked whether the absence of regular-verb priming could be explained by the phonological relationship between prime and target, by looking for the corresponding absence of two phonological priming effects, one in which prime and target were related by the inflectional rhyme pattern of the regular past tense, and another in which prime and target were related by other kinds of phonological and orthographic overlap. Third, we asked whether such regular-irregular dissociations would be better described as categorical or graded. Finally, we asked whether the above effects could be captured with event-related potentials, with a focus on the N400 and LPC components to address whether lexical or post-lexical processes were disrupted in the patient group. We consider each of these in turn.

(1) Does the priming of regular and irregular verbs dissociate following damage to Broca's area?

Regarding the first major question posed by this paper, the previously observed dissociation between regular- and irregular-verb priming (Marslen-Wilson & Tyler, 1997; Tyler et al., 2002a) was replicated in the response time data of the current study. As a group, controls demonstrated significant priming of 44 ms for regular verbs ($p=.002$), as well as significant – and significantly greater – priming of 102 ms for irregular verbs ($p<.001$). No differences in the error rates for regular and irregular verbs were observed (1.1% and 0.7%, respectively). As a group, patients with damage to Broca's area demonstrated a non-significant priming effect of 5 ms for regular verbs ($p=.82$) and a significant – and significantly greater – priming effect of 98 ms for irregular verbs ($p<.001$). As before, no differences in the error rates for regular and irregular verbs were observed (1.8% and 2.5%, respectively). We note that in a direct comparison of controls and patients, there was only a trend for the regular-verb priming effect to be smaller for the patients compared to the controls ($p=.10$).

These findings permit a stronger connection to be drawn between damage to Broca's area and the disruption of regular-verb priming than was possible in the studies of Marslen-Wilson and Tyler (1997; Tyler et al., 2002a). The patients in those studies had extremely diverse left-hemisphere lesions that extended well beyond the LIFG. The eleven patients included here were selected on the basis of damage to Broca's area, defined as the pars opercularis (BA 44) and pars triangularis (BA 45) of the LIFG. The present study also complements the finding of a correlation between tissue density in the LIFG and the size of regular-verb priming effects that was found in a study of 22 brain-lesioned patients who were unselected for lesion location (Tyler et al., 2005a).

Despite the relative lesion homogeneity of the current patient group, not all patients were equivalent with regard to the regular-verb priming effect (Figure 2). Some of the LIFG patients demonstrated preserved regular-verb priming effects of as much as 99 ms (Patient 5). However, other patients demonstrated either flat effects (as in Tyler et al., 2002a) or inhibitory effects (as in Marslen-Wilson & Tyler, 1997) of as much as 155 ms (Patient 7),

thus reducing the mean effect for the group. As with the controls, the difference between the priming effects for regulars and irregulars in the patient group was fairly consistent, with everyone except for Patient 6 showing a numerically greater priming effect for irregulars compared to regulars. Neither the lesion extent outside of Broca's area nor the aphasia subscores on the Western Aphasia Battery provides a clear explanation for this variation in regular-verb priming or any of the behavioral effects.

At face value, the lack of significant regular past-tense priming is consistent with the dual-system perspective (e.g., Pinker, 1999; Pinker & Ullman, 2002; Marslen-Wilson & Tyler, 1998), including its IRP variant (Marslen-Wilson & Tyler, 2007), that the perception and lexical access of regular past tenses involves an affix-stripping process that is dependent on Broca's area, whereas irregular past tenses can bypass this process and be retrieved directly from the mental lexicon. However, the single-system perspective also offers explanations for this dissociation, with specific predictions about the relationships between morphological and ortho-phonological priming, as well as a prediction that the dissociation should be graded and not categorical (e.g., Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003).

(2) Is the regular-irregular dissociation related to phonological factors, and if so, does the inflectional rhyme pattern have special status?

Two control conditions were included in the experiment to examine word-onset ortho-phonological priming. The pseudopast condition (*bead-bee*) was designed to mimic the inflectional rhyme pattern between regular past- and present-tense forms, which is argued to hold a special morpho-phonological status in the IRP viewpoint of Marslen-Wilson and Tyler (2007). This approach predicts that regular-verb priming effects should pattern with pseudopast priming effects, given that only conditions in which an inflectional rhyme pattern is present should trigger an attempt at LIFG-dependent morphological segmentation. In contrast, the orthophono condition (*barge-bar*), while representing a similar degree of ortho-phonological overlap between prime and target, did not signal a potential morphological relationship. The IRP viewpoint predicts that this condition should not implicate LIFG-dependent processing and as a result, orthophono priming effects should be distinct in pattern from those of the regular verbs and pseudopasts. However, single-system approaches that emphasize a link between regular morphology and phonology (e.g., Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003), might predict that all three priming effects – regular verbs, pseudopast, and orthophono – should group together.

The behavioral data straightforwardly support the latter pattern. Whereas the controls demonstrated significant priming effects for all three of these conditions, the patients with damage to Broca's area did not demonstrate significant priming for any of them. By examining individual variability in priming, it can further be shown that the size of the regular, pseudopast, and orthophono priming effects all correlate significantly with one another. These data suggest that the reduced priming effect for regular verbs following damage to Broca's area is based in a reduction of the phonological priming effects that we observe in this design. Contrary to the prediction of the IRP viewpoint, this relationship was not specific to the condition that contained the regular inflectional rhyme pattern (the pseudopast condition), but rather extended to other kinds of phonological and orthographic overlap that did not signal morphological relationships (the orthophono condition). Instead, the relationship between regular morphology and phonology more generally is consistent with the argument that deficits in regular morphology are based in deficits of phonological processing.

(3) Is the regular-irregular dissociation better described as categorical or continuous?

Patients with damage to Broca's area demonstrated preserved priming for irregular verbs in this experimental design. This result is predicted both by dual-system viewpoints, including the IRP variant, and by single-system viewpoints, but for different reasons. From a dual-system perspective, the preserved effect is the result of the irregular past-tense forms having distinct representation in the mental lexicon, thus bypassing the supposed impairment in regular morphological processing. From a single-system perspective, the preserved irregular priming effect is the result of a stronger dependence on semantic representations in linking the past- and present-tense forms, and a weaker dependence on phonological representations, which are supposedly compromised.

In considering the nature of this preserved irregular-verb priming, we divided the irregular verbs into two groups – weak irregular verbs and strong verbs – and compared these two classes with the regular verbs. In the case of the controls, the regular-irregular difference is better described as a weak-strong difference, with regular-verb (44 ms) and weak-irregular-verb effects (58 ms) grouping together statistically and each being different from that of the strong verbs (162 ms). In the case of the patients, the regular-irregular difference is better described as a three-way split between regular verbs (5 ms), weak irregular verbs (74 ms), and strong verbs (154 ms), all of which were significantly different from one another. These results suggest that the regular-irregular dissociation is graded and continuous, not categorical (see Justus et al., 2008, 2009; Joanisse & Seidenberg, 1999, 2005; Kiehl et al., 2008; Kiehl & Joanisse, 2010; also see Hay & Baayen, 2005).

These results are problematic for dual-system theories, which argue for a categorical distinction between the processing of regular and irregular verbs. From this perspective, regular verbs are processed according to a linguistic rule that adds or strips the suffix $[-d]$, realized as one of three different allomorphs ($/d/$, $/t/$, or $/Id/$), to or from the present-tense stem. These rule-based morphological processes come into play only for the class of regular verbs, and cannot be applied to the irregulars, which must be fully listed in lexical memory. Even the weak irregular verbs – those that end in $/t/$ or $/d/$ in the past tense, often as the result of affixation – are not processed based on linguistic rules, but are memorized just as the strong verbs are. Most dual-system perspectives (e.g., Pinker, 1999; Pinker & Ullman, 2002) therefore predict that any dissociations in the processing of regular and irregular verbs should be categorical, with all regular verbs grouping together and all irregular verbs grouping together, regardless of whether they are weak or strong.

The predictions of the IRP viewpoint (Marslen-Wilson & Tyler, 2007) are less clear. One might argue that this view predicts that regular-irregular dissociations should be categorical, given that IRP is clearly aligned with the dual-system framework of morphological decomposition for regular verbs only. However, one might also argue that the IRP viewpoint can accommodate some continuous dissociations. For instance, it is possible that the phonology of the weak irregular past tenses could gain them access to the same LIFG-dependent morphological segmentation mechanisms proposed for regular verbs, resulting in an attempt at morphological segmentation (see Post et al., 2008). In the current study, about half of the weak irregular past tenses contained the inflectional rhyme pattern (e.g., *slept*, but not *spent*). However, this would be a more plausible explanation for why such words might prime – or fail to prime – the corresponding nonword that would result from IRP-triggered morphological decomposition (e.g., *slept-slep*), and not the true present-tense form (e.g., *slept-sleep*).

The continuous regular-irregular dissociation that we report here is particularly consistent with single-system theories, because the result was specifically predicted. Single-system theories argue that the processing of all verb morphology, both regular and irregular forms,

entails the mapping between form (phonology and orthography) and meaning (semantics), and that morphological relations between words are emergent and reflect interactions between these relationships (see Gonnerman et al., 2007). This perspective eschews the idea of discrete linguistic rules, and instead embraces the notions of distributed knowledge representation and probabilistic processing. The single-system perspective predicts that any dissociations in the processing of regular and irregular verbs should be graded and continuous, and rooted in differences in the ortho-phonological and semantic relationships between present- and past-tense forms.

(4) Does the regular-irregular dissociation extend to event-related potentials?

Unlike in the behavioral data, the ERP priming effects for both regular and irregular verbs were similar to each other for both patients and controls (Figure 3). Considering the overall comparison of regular and irregular verbs, some subtle differences were observed: for both controls and patients, the priming effect was significant for both regulars and irregulars during an earlier 350–600 ms window targeting the N400, but either remained significant or trended in this direction for the irregulars only during a later 600–850 ms window targeting the LPC. Although the differential size of the two effects did not reach significance, as in our study of healthy young controls (Justus et al., 2008), the trend is consistent with the argument of that study, as well as the current behavioral data, that irregulars prime more strongly in this experimental design. The more critical question for our purposes, however, concerns whether the N400 verb-priming effect differed between controls and patients, and whether this interacted with verb regularity. Neither of these effects was observed; the patients demonstrated N400 priming effects for both verb types, just as the controls did.

The lack of a regular-irregular dissociation in the N400 data of the patients, despite a dissociation in the response time data, suggests that these two dependent measures do not reflect the same cognitive processes. The absence of significant correlations between the RT and N400 priming effect sizes also supports this idea. The preservation of the regular-verb N400 priming effect in the patients suggests that the lexical entries for the present-tense targets were successfully pre-activated by the past-tense primes. Therefore, the absence of behavioral regular-verb priming may not be attributable to a disruption of lexical access resulting from compromised morphological parsing mechanisms, as argued by Marslen-Wilson and Tyler (2007), because this leads to the prediction of reduced regular-verb N400 priming. Similarly, the absence of behavioral regular-verb priming may not be attributable to changes in pre-lexical and lexical priming based on ortho-phonological overlap, because this arguably also leads to the prediction of reduced regular-verb N400 priming. Instead, the absence of behavioral regular-verb priming may be due to altered post-lexical processes following the N400. These post-lexical processes might still be impacted by ortho-phonological overlap between primes and targets, given the relationships in the behavioral data between the priming of regular verbs and that of the pseudopast and orthophono conditions.

The relative timing of the N400 and the behavioral response can be accommodated in this hypothesis. For both controls and patients, the differences between the N400 for primed and unprimed items began to emerge as early as 350 ms following the onset of the target words, which had a mean duration of 514 ms. Thus, the N400 priming effect began before the target word had been completely uttered. These effects resolved and returned to the baseline provided by the unprimed ERPs by 850 ms (in the case of the irregular verbs), if not sooner. In contrast, the grand mean response times of 866 ms following word onset for the controls, and 1130 ms following word onset for the patients, suggest that the behavioral response could reflect additional processing following the N400 and lexical access. A further suggestion from the behavioral data that the lack of priming for regular verbs may have arisen post-lexically is the significant relationship between participants' mean response

times and the size of the three priming effects that were diminished in the patient group as a whole. The longer the participants took, in general, to perform the lexical decision task, the smaller the priming effects were for regular verbs and the two phonological control conditions (each $p < .002$). The size of the irregular-verb priming effect was not correlated with mean response time ($p = .60$).

The interpretation of the ERP data from the pseudopast and orthophono conditions is less clear. In our study of young controls in this experimental design, we observed reduced N400s for prime-target pairs that shared word-onset ortho-phonological overlap when both prime and target were presented in the auditory modality (Justus et al., 2008), as in the current study. When presentation was cross-modal, with auditory primes and visual targets, N400 effects were minimized and a post-lexical anterior negativity (PLAN), which affected the late positive component (LPC) of the waveform, became more prominent (Justus et al., 2009). We suggested that the PLAN might reflect a relatively late, strategic process driven by word-onset ortho-phonological overlap between primes and targets. If such post-lexical processes were disrupted in the patients, as suggested above, this might lead to the prediction that that N400 effects would be preserved for the phonological conditions, but PLAN modulations of the LPC would be altered.

We observed evidence for both N400 and PLAN effects in the current study, with differences between the controls and patients, and between the pseudopast and orthophono conditions. Specifically, during the N400 window, the controls demonstrated only a trend for an effect, and only for the pseudopast condition ($p = .07$). In contrast, the patients demonstrated significant effects for both the pseudopast and orthophono conditions (each $p < .01$), indicating that, like the controls of Justus et al. (2008), hearing a prime word facilitated the lexical access of a target word with which it shared word-onset ortho-phonological overlap. Why this effect would be diminished in the age-matched controls, relative to the young controls of the earlier study, and yet be preserved in the patients is unclear. Any effect of aging (see Federmeier & Kutas, 2005) would be expected to apply to both groups of the current study.

During the LPC window, the controls demonstrated a marginal reversal of the N400 effect over anterior electrodes (i.e., the PLAN), but only for the pseudopast condition ($p = .06$). In contrast, the patients demonstrated a continuation of the N400 effect, but only for the orthophono condition ($p = .04$), while a weak trend for a PLAN-direction reversal failed to approach significance. Given that the N400 effects for primed items are more positive, and the PLAN effects are more negative, the overlap between the two could cause each one to cancel out the other. We speculate that this may be the reason why the controls did not show significant N400 reductions for the pseudopast and orthophono conditions, i.e., the already evolving PLAN effects obscured them. In contrast, if PLAN effects were diminished in the patients, this would make the remaining N400 effects more prominent.

Despite the unresolved questions regarding the PLAN effects on the late positive component, the ERP data clearly indicate preserved N400 priming for both regular and irregular verbs in both LIFG patients and controls. This suggests that despite damage to the LIFG, patients are able to pre-activate the lexical representations for regular present-tense forms (e.g., *look*) when they hear the corresponding past-tense form (*looked*). This result is in direct conflict with the notion of Marslen-Wilson and Tyler (2007) that, when hearing a regular past-tense form, lexical access for the corresponding present tense is dependent upon an LIFG-dependent mechanism to detect the regular inflectional affix and strip it from the stem. The implications of our N400 results are either that affix-stripping is not critically dependent on the LIFG, or, as argued by single-system models, that affix-stripping is not necessary given that all past-tense forms would be represented in the lexicon. The result is

also problematic for any single-system account that would require the effects of ortho-phonological overlap in this experimental design to occur prior to lexical access.

Implications for Theories of Broca's Area Function

The discussion to this point has been framed in terms of two competing views of Broca's area function, as viewed from the perspective of the past-tense debate. Dual-system theories view the function of this region as morphological. This view is aligned with the notion that Broca's area is needed for grammatical processing more generally, including not only morphological but also syntactic processing (Pinker, 1999; Pinker & Ullman, 2002; Marslen-Wilson & Tyler, 1998). In contrast, single-system theories view the function of this region as phonological. This view is aligned with the notion that Broca's area is needed for speech processing, including not only speech production but also speech perception (Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Bird et al., 2003). Although our experiment was designed with the specific predictions of single- and dual-system theories in mind, moving beyond the narrow focus of the past-tense debate may help explain two unexpected findings from the present experiment: (1) despite behavioral regular-verb priming being diminished in the LIFG group, the corresponding N400 priming effects were preserved, and (2) the expected relationships between the regular-verb, pseudopast, and orthophono priming co-varied with overall RT for the lexical decision task, such that patients who took longest to respond tended to show reduced behavioral priming for these three effects. Table 3 presents eleven hypotheses concerning the function of Broca's area – along with two hypotheses for the deficit underlying non-fluent aphasia – and a prediction concerning how disruption to each hypothesized function might impact the two-word past-tense priming design. The first two rows represent the phonological and morphological views discussed thus far.

Although not typically cited by single-system authors, the view that Broca's aphasics have a generalized phonological deficit parallels aspects of Blumstein and colleagues' view that Broca's aphasics have a deficit in using phonological information to perform lexical access. For instance, Broca's aphasics showed a reduction in priming between semantically related words when the initial phoneme of the prime word was phonetically altered (e.g., *c*at-dog*) or replaced by another (e.g., *gat-dog*) (Milberg et al., 1988; Aydelott Utman et al., 2001; Misiurski et al., 2005; for a review see Blumstein, 2007; also see Janse, 2006, 2008). Thus, regarding the present two-word priming design, this view might also predict a reduction in word-onset ortho-phonological priming, which would account for reductions in behavioral priming effects for the regular-verb, pseudopast, and orthophono conditions, with relative preservation of irregular-verb priming. However, like Bird et al. (2003) and Marslen-Wilson and Tyler (2007), this view would seem to attribute phonological priming to pre-lexical events, and accordingly, would also predict corresponding reductions in N400 priming, which was instead preserved.

We next consider two proposed roles of Broca's area in lexical-semantic processing, reflecting neural events that occur during or immediately following the N400. It has been proposed that the LIFG, especially BA 44, is a candidate region for so-called mirror neurons (Rizzolatti et al., 2001), though it has been argued that evidence for this in humans is rather weak (Hickok, 2009). Nevertheless, this view might suggest that lexical activation and associated lexical priming effects would be altered for verbs that refer to imaginable actions, particularly actions performed by the hand or arm. However, such items in our stimulus list were split roughly equally between the regular (e.g., *reached*, *placed*, *grabbed*) and irregular lists (e.g., *dealt*, *threw*, *wrote*), and would not seem to account for a reduction in behavioral priming for the regular items alone.

A strong case can be made for a role for Broca's area in resolving lexical-semantic ambiguity for word-forms that are associated with more than one lexical entry (e.g., Rodd et al., 2005; Davis et al., 2007; Zempleni et al., 2007; Bedny et al., 2007). This might suggest that lexical activation and associated lexical priming effects for ambiguous words would be altered. While we attempted to avoid such items in designing our regular, pseudopast, and orthophono conditions, a few items may be considered lexically ambiguous. In contrast, many of the irregular past-tense items were unavoidably lexically ambiguous (e.g., *made*, *left*, *read*). However, an interpretation based in lexical ambiguity would not seem to explain a relative reduction in priming for the regular items, as observed in the present study.

In addition to claims regarding morphological processing, Broca's area is frequently associated with syntactic processing (see Sahin et al., 2006). Potential roles for the region in syntax include syntactic parsing (e.g., Friederici, 2002), syntactic movement (Grodzinsky, 2000; Grodzinsky & Santi, 2008), or the checking of thematic-role assignments (Caplan et al., 2008). Such syntactic roles, along with the literature on semantic ambiguity, were integrated by Hagoort (2005) in a memory-unification-control (MUC) framework. In this view, the LIFG plays an essential role in unification, i.e., "the integration of lexically retrieved information into a representation of multi-word utterances" (2005, p. 416). While it is clear that syntactic roles, and other views that entail the binding of words together in utterances, need to be accounted for in any general theory of Broca's area function, the predictions of these viewpoints for the two-word priming design are unclear.

The final four rows of Table 3 represent proposed functions of the LIFG that may potentially explain altered patterns of behavioral priming that are due to events following lexical access. Broca's area plays a role in verbal working memory, and has typically been associated with articulatory rehearsal within the Baddeley (1986) phonological-loop framework (e.g., Paulesu et al., 1993; Baldo & Dronkers, 2006). Some have argued that the role of Broca's area in syntactic processing may be best explained in terms of verbal working memory (Kaan & Swaab, 2002; Rogalsky & Hickok, in press). With regard to the current design, it is possible that, while not required by the task instructions, healthy participants verbally rehearse the prime word in anticipation of the target. Given the duration of the ISI between prime and target (on average 870 ms), this would likely amount to a single covert articulation of the prime word. This could be the basis of at least part of the priming effects driven by phonological overlap that were observed in the control group, but were absent in the LIFG patient group, due to a diminished ability to articulate the prime word covertly during the interval between prime and target. In contrast, patterns of activation within the mental lexicon would be unchanged, and give rise to intact N400 priming effects in both groups.

A focus on covert articulation following lexical access is also consistent with the speech comprehension model of Hickok and Poeppel (2004, 2007). According to these authors, speech comprehension and lexical access in naturalistic situations depend upon a ventral processing stream projecting through the temporal lobe. Only speech perception tasks that have specific task demands, such as the need for explicit sub-lexical segmentation (see Burton, 2001, 2009) will recruit a dorsal stream that projects to inferior frontal regions, and which is also used during speech production. From the perspective of the Hickok-Poeppel model, neither the dual-system notion that the LIFG is necessary for parsing heard inflectional morphemes (Marslen-Wilson & Tyler, 2007), nor the single-system notion that the LIFG is necessary for phonological aspects of spoken-language processing (Bird et al., 2003) would be predicted. Instead, this view might suggest that any effects of LIFG damage on performance in an auditory lexical priming task would be due to task demands and explicit strategies. For instance, healthy participants may become consciously aware of the morpho-phonological relationships between primes and targets, and develop a strategy to

anticipate likely targets by explicitly segmenting the final phonemes of the prime words (see McQueen & Sereno, 2005), recruiting the articulatory mechanisms of the LIFG (see Burton, 2001, 2009). Such a strategy would contribute to priming for the regular, pseudopast, and orthophono conditions, and to a lesser extent, the weak-irregular condition. Given their problems with covert articulation, people with LIFG damage would not benefit from such segmentation strategies, which would impact response times for these conditions. Again, automatic lexical priming within the temporal lobe would be intact, accounting for the preserved N400 priming effects.

The final two theories listed in Table 3 also may be able to account for changes in behavioral priming related to overall RT and accompanied by preserved N400 priming. These theories argue for a more domain-general role in cognitive control for the LIFG, which in this literature is often referred to as the ventrolateral prefrontal cortex (VLPFC). One such view is that the LIFG, particularly the pars orbitalis (BA 47), supports controlled retrieval of goal-relevant representations (Badre & Wagner, 2007). For instance, the LIFG has been implicated in two-word semantic priming designs only when the interval between prime and target is relatively long (e.g., 1000 ms), arguably permitting strategic retrieval in addition to automatic lexical activation (Gold et al., 2006). This finding echoes an earlier debate in the patient literature concerning whether the performance of Broca's aphasics in these tasks is better explained in terms of altered automatic or controlled processes (see Milberg et al., 1995; Tyler et al., 1995; Hagoort, 1997). The notion of controlled retrieval is also particularly relevant for the role of Broca's area in the past-tense production task described in the Introduction; Broca's area is recruited for the production of both regular and irregular past tenses, and especially so for irregulars. From a single-system perspective, the less consistent phonological mapping between irregular present- and past-tense forms might be expected to lead to a greater need for controlled retrieval (Seidenberg & Arnoldussen, 2003). From a dual-system perspective, greater cognitive control might be expected for the production of irregular past tenses, because the speaker may be inhibiting an over-regularization (Beretta et al., 2003a).

Another hypothesis regarding the LIFG/VLPFC in cognitive control is that this region detects and resolves conflict between competing representations (Novick et al., 2005; Thompson-Schill et al., 2005). In the two-process view of Badre and Wagner (2007), this role is ascribed to the pars triangularis (BA 45). The conflict-resolution view is notable in that it integrates a variety of seemingly disparate results into a unified view of LIFG function; findings in phonological ambiguity, semantic ambiguity, and syntactic ambiguity are grounded in a larger literature implicating the LIFG in representational-interference designs such as the Stroop (January et al., 2009). For instance, in the Sternberg item-recognition task, participants view a group of letters and then must respond to a probe item to indicate whether it was part of the immediately preceding set. In a modification designed to create proactive interference, representational and response conflict can be manipulated depending on whether the target item was also a part of the memory set of the preceding trial, leading to increased recruitment of the pars triangularis (Jonides & Nee, 2006). Some patients with focal lesion to the LIFG have difficulty specifically with these trials (Thompson-Schill et al., 2002; Novick et al., 2009). In the current study, we speculate that representational conflict may occur when a prime-target pair that differs by a single phoneme is presented. Healthy controls may have no difficulty inhibiting or directing attention away from the representation of the prime in order to respond to the target, regardless of the phonological similarity of the two items. In contrast, patients with impaired cognitive control may have difficulty with phonologically similar primes and targets due to a representational conflict between the two.

Two results of the current study, while being the most unexpected with regard to the predictions of dual- and single-system models, are intriguing in light of these last four views of LIFG function. The first is the observation that the absence of regular-verb priming in the patients' behavioral data was not accompanied by any reduction in N400 priming, a result which might have been expected from both dual- and single-system perspectives. The second observation is the significant relationship between the three priming effects that were abolished in the LIFG patient group (i.e., priming for regular verbs, pseudopast, and orthophono) and the amount of time in general a participant required to perform the lexical decision task, which is not easily accounted for by either dual- or single-system views. Both of these results suggest that the "deficit" that the LIFG patients have with the regular past tense and the phonological control conditions is not intrinsic to the perception of these word forms, but rather is an effect that emerges following lexical access in this particular experimental design. As our brief review indicates, these effects instead could be based in previously well documented functions of the LIFG in speech production (covert articulation, segmentation strategies) and/or cognitive control (controlled retrieval, representational conflict).

Conclusion

Here we replicated a previously reported dissociation between disrupted regular-verb priming and preserved irregular-verb priming following brain damage. That our eleven patients were chosen based on documented damage to Broca's area strengthens the argument that this dissociation is a consequence of damage to the LIFG. Examination of the behavioral data revealed that absent regular-verb priming covaried with absent ortho-phonological priming, regardless of whether phonological cues to morphological structure were present. Further, a division of stimuli into regular, weak irregular, and strong verbs suggested that the regular-irregular dissociation was continuous, rather than categorical. Both of these results are predicted by the single-system, connectionist approach to inflectional morphology and are not predicted by current dual-system, rule-based models. Event-related potential data demonstrated that N400 priming effects were intact, suggesting that the absence of significant regular-verb priming in the behavioral data of these patients was not the result of impairments in pre-lexical or lexical priming, and was instead the result of post-lexical events related to covert articulation, segmentation strategies, and/or cognitive control.

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Lesion Reconstructions

Figure 1.

Brain lesions of each of the eleven patients with damage to Broca's area, defined as the pars opercularis (BA 44) and pars triangularis (BA 45) of the LIFG, are shown in red on a standard brain image. An overlay of the eleven brain lesions illustrates the regions of maximum overlap in the LIFG and insula. These images were produced using MRICro (Rorden & Brett, 2000).

Figure 2.

Response time data, first as a function of Word Type (upper four plots) and second for the irregular verbs alone, separated into weak irregular verbs and strong verbs (lower four plots). Controls are presented to the left and patients to the right. Bar graphs illustrate the grand mean response times for each group, with error bars representing standard error. Scatter plots illustrate individual response time data, using a difference score in order to represent each person by a single point. Horizontal bars represent the mean difference for the group.

Figure 3.

ERPs to target words within the nine-electrode region of interest, demonstrating the N400 effect as a function of Word Type (regular verbs, irregular verbs, pseudopast, and orthophono) and Priming. Controls are presented to the left and patients to the right.

Figure 4. Topographic maps of the scalp distributions displaying the N400 priming effect (unprimed-primed) between 350–600 ms and 600–850 ms as a function of Word Type (regular verbs, irregular verbs, pseudopast, and orthophono) and Priming. Controls are presented to the left and patients to the right.

Table 1

Participants

Patient	Sex	Age	Ed.	Years Post	% Pars Oper.	% Pars. Trian.	% Pars Orbit.	% Insula	WAB Fluency	WAB Comp.	WAB Rep.	WAB Naming	WAB Type
P1	F	54	17	4	7	47	9	19	10	9.80	10.0	9.5	WNL
P2	F	63	18	6	91	50	6	58	9	8.85	8.8	8.9	anomic
P3	M	68	20	2	79	41	5	71	10	10.00	9.8	9.5	WNL
P4	F	69	15	4	98	64	33	73	9	9.75	9.4	8.8	anomic
P5	M	36	13	6	99	93	73	99	2	9.45	5.4	8.9	unclass.
P6	M	42	18	3	97	95	10	64	9	8.70	8.9	9.3	unclass.
P7	M	65	12	16	100	100	81	99	6	8.90	9.4	6.3	anomic
P8	M	65	16	12	86	60	96	100	4	10.00	5.2	6.5	Broca
P9	M	72	12	8	100	49	2	53	9	9.95	9.4	9.0	WNL
P10	F	47	20	7	100	100	97	90	9	10.00	8.6	9.2	unclass.
P11	M	54	16	8	100	98	56	74	5	9.20	7.5	8.7	anomic
Patient Group	4F, 7M	58 +/- 12	16 +/- 3	7 +/- 4	87	72	43	73	7	9.51	8.4	8.6	4 anomic, 1 Broca, 3 unclass., 3 WNL
Control Group	3F, 8M	57 +/- 12	16 +/- 3										

Table 2

Auditory immediate-priming design with lexical decision

Word Type	Priming	Prime	Target	Target Freq. **	Target Length
Regular verbs (n = 150)	Primed	<i>looked</i>	<i>look</i>	1.94 +/- 0.4	528 +/- 92 ms
	Unprimed	<i>worked</i>	<i>seem</i>	1.94 +/- 0.4	523 +/- 78 ms
	Nonword	<i>asked</i>	<i>*tarb</i>		
Irregular verbs (n = 150)	Primed	<i>spoke</i>	<i>speak</i>	1.98 +/- 0.8	515 +/- 92 ms
	Unprimed	<i>bound</i>	<i>wake</i>	1.98 +/- 0.8	518 +/- 81 ms
	Nonword	<i>took</i>	<i>*plinn</i>		
Pseudopast (n = 150)	Primed	<i>bead</i>	<i>bee</i>	1.61 +/- 1.1	516 +/- 53 ms
	Unprimed	<i>bulb</i>	<i>pie</i>	1.59 +/- 1.1	522 +/- 65 ms
	Nonword	<i>deer</i>	<i>*cleeth</i>		
Orthophono (n = 150)	Primed	<i>barge</i>	<i>bar</i>	1.29 +/- 0.9	494 +/- 70 ms
	Unprimed	<i>bribe</i>	<i>tea</i>	1.21 +/- 0.8	496 +/- 64 ms
	Nonword	<i>pouch</i>	<i>*grwal</i>		

**
log lemma frequency per million, +/- s.d.

Table 3

Theories of Broca's Area / LIFG Function

Role of Broca's Area / LIFG	Reference	Effect of Disruption on Past-Tense Priming
* Phonological processing (perception and production)	Bird et al., 2003	Disrupted phonological representation, reduced phonological priming
Morphological parsing	Marslen-Wilson & Tyler, 2007	Disrupted segmentation of regular past-tense IRP into stem and affix
* Lexical activation, competition, and suppression	Blumstein, 2007 Janse, 2006	Reduced lexical activation, reduced phonological priming, increased interference
Lexical-semantic ambiguity resolution	Rodd et al., 2005 Bedny et al., 2007	Altered priming for lexically ambiguous items
Action semantics	Rizzolatti et al., 2001	Altered priming for words describing imaginable actions
Syntactic parsing	Friederici, 2002	[No clear prediction for two-word priming]
Syntactic movement	Grodzinsky, 2000	[No clear prediction for two-word priming]
Thematic-role checking	Caplan et al., 2008	[No clear prediction for two-word priming]
Unification	Hagoort, 2005	[No clear prediction for two-word priming]
Working memory, articulatory rehearsal	Paulesu et al., 1993 Baldo & Dronkers, 2006	Disrupted covert articulation, reduced phonological priming
Speech production, explicit segmentation	Hickok & Poeppel, 2007 Burton, 2001, Burton, 2009	Disrupted task strategies involving explicit sub-lexical segmentation
Controlled retrieval	Badre & Wagner, 2007 Gold et al., 2006	Disrupted controlled components of priming and lexical retrieval
Representational conflict detection and resolution	Novick et al., 2005 Thompson-Schill et al., 2005	Increased proactive interference between phonologically similar primes and targets

* Hypothesized deficit in nonfluent or Broca's aphasia, which is not necessarily the result of damage to Broca's area in the LIFG.