ABSTRACT GRAMMATICAL PROCESSING OF NOUNS AND VERBS IN BROCA'S AREA: EVIDENCE FROM fMRI

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ABSTRACT

The role of Broca's area in grammatical computation is unclear, because syntactic processing is often confounded with working memory, articulation, or semantic selection. Morphological processing potentially circumvents these problems. Using event-related functional magnetic resonance imaging (fMRI), we had 18 subjects silently inflect words or read them verbatim. Subtracting the activity pattern for reading from that for inflection, which indexes processes involved in inflection (holding constant lexical processing and articulatory planning) highlighted left Brodmann area (BA) 44/45 (Broca's area), BA 47, anterior insula, and medial supplementary motor area. Subtracting activity during zero inflection (*the hawk; they walk*) from that during overt inflection (*the hawks; they walked*), which highlights manipulation of phonological content, implicated subsets of the regions engaged by inflection as a whole. Subtracting activity during verbatim reading from activity during zero inflection (which highlights the manipulation of inflectional features) implicated distinct regions of BA 44, 47, and a premotor region (thereby tying these regions to grammatical features), but failed to implicate the insula or BA 45 (thereby tying these to articulation). These patterns were largely similar in nouns and verbs and in regular and irregular forms, suggesting these regions implement inflectional features cutting across word classes. Greater activity was observed for irregular than regular verbs in the anterior cingulate and supplementary motor area (SMA), possibly reflecting the blocking of regular or competing irregular candidates. The results confirm a role for Broca's area in abstract grammatical processing, and are interpreted in terms of a network of regions in left prefrontal cortex (PFC) that are recruited for processing abstract morphosyntactic features and overt morphophonological content.

Key words: morphology, language production, speech production, regular/irregular inflection, grammar, syntax, morphosyntax, morphophonology, insula, anterior cingulate

INTRODUCTION

Broca's area may be the most widely known region of the brain, and its discovery in 1861 as a major component of language ability marks the beginning of modern neuropsychology. Nonetheless, after more than a century, neither the function of Broca's area nor the neural substrates of language are well understood. In the experiments described here we measured the neural activity underlying a simple linguistic task, yielding evidence that Broca's area is (among other things) central to abstract grammatical computation.

Relation of Broca's Area to Grammatical Processing and Other Functions

Early in the study of the aphasias, patients with lesions to Broca's area were observed to be impaired in speech production, especially in the omission or misuse of inflections and other closed-class morphemes, but seemingly intact in speech comprehension (Broca, 1861). This led to the view that that Broca's area handled expressive as opposed to receptive language (Wernicke, 1874; Geschwind, 1970), and became a central assumption of the Wernicke-Geschwind model of language organization in the brain. It was subsequently challenged by the demonstration that Broca's aphasics were unable to comprehend sentences whose meanings could not be accessed by simple word order but only by an analysis of grammatical structure (e.g., *the boy that the girl is chasing is tall*) (Zurif et al., 1972; Caramazza and Zurif, 1976). This led to the hypothesis that Broca's area subserves the computation of grammar, both receptive and expressive (Caramazza and Zurif, 1976; for review, see Dronkers et al., 2000). The hypothesis, if true, would play a major role in our understanding of language, because grammatical computation, by combining a finite set of memorized elements into novel sequences, is what gives language its infinite expressive power. Furthermore, because grammatical computation is the ability that most clearly differentiates human language from animal communication (Nowak et al., 2000; Fitch and Hauser, 2004; Pinker and Jackendoff, 2005), identifying its neural substrate is central to the study of language and human cognition in general.

This equation of Broca's area with grammar was challenged by Linebarger et al. (1983a), who showed that classic Broca's aphasics could make well-formedness judgments that hinged on subtle aspects of grammatical knowledge, such as the rules governing prepositions, particles, and other closed-class morphemes (e.g., *She went the stairs*

up in a hurry). Broca's aphasics' ability to recognize that a sentence needs certain closed-class morphemes, combined with an inability to use those morphemes to understand the sentence, has been called the "syntax-there-but-not-there" paradox (Linebarger et al., 1983b; Cornell et al., 1993). One possible resolution is that only a circumscribed subset of grammar is computed in Broca's area and impaired by Broca's aphasia, such as the building of tree structures or the linking of elements in different parts of the sentence that refer to the same entity, as in anaphora and the binding of traces (Cornell et al., 1993). For example, Grodzinsky (1986a, 1986b, 2000) argues that the manipulation of traces is the only thing computed in Broca's area, and that Broca's aphasia results from deletion of the traces. Another is to suggest that Broca's area is involved in certain aspects of the on-line processing of grammar but not underlying grammatical knowledge (see Linebarger et al., 1983a; Zurif and Grodzinsky, 1983). Yet another is to underscore the heterogeneity of deficits labeled "Broca's aphasia", a consequence of the uniqueness of individual patients' lesions and the complexity and variation of the language circuitry of the brain (Berndt and Caramazza, 1999).

The recent advent of functional neuroimaging to complement lesion studies has pinpointed neither the function of Broca's area nor the substrate of grammatical computation. A set of studies by Stromswold et al. (1996) and Caplan and Waters (1999) reinforced an association between the two. They presented subjects with sentences containing identical words and the same kind of meaning but varying in syntactic complexity, such as relatively easy right-branching sentences (e.g., *The child spilled the juice that stained the rug*) and more difficult center-embedded sentences (e.g., *The juice that the child spilled stained the rug*). Regional cerebral blood flow (rCBF), measured by positron emission tomography (PET), showed significant differences only in Brodmann area (BA) 44, the *pars opercularis* of Broca's area. This finding does not, however, show that Broca's area is responsible for grammatical knowledge and processing. The two kinds of sentences are, in many theories of grammar, grammatically similar or identical, and differ only in the demands they make on working memory in sentence parsing, such as how long a person has *juice* in memory before encountering the predicates (in this example, *enjoy* or *stain* or both) that indicate its semantic role. In a recent review, Kaan and Swaab (2002) note that Broca's area shows increased activity not only to contrasts such as right-branching *versus* center-embedded sentences, but to sentences with ambiguous words, low-frequency words, or the need to maintain words over extended distances. They conclude that Broca's area is sensitive to any increase of processing load, rather than being dedicated to

linguistic computation. They argue that other findings tying Broca's area to syntax can also be reinterpreted in terms of generic processing load, including comparisons of reading sentences *versus* word lists, studies of the reading of Jabberwocky sentences (consisting of meaningless words in grammatical structures), and studies on the detection of syntactic errors. Kaan and Swaab (2002) argue not only against the strong hypotheses that only Broca's area processes syntax and that Broca's area only processes syntax, but against the weaker hypothesis that Broca's area is systematically involved in grammatical computation at all. They conclude that "Broca's area is only systematically activated when processing demands increase due to working memory demands or task requirements". Similar conclusions are found in Just and Carpenter (1992) and Bates and Goodman (1997), who note that because general working memory demands increase in comprehending complex sentences, the seeming grammatical difficulties of Broca's aphasics could be attributable to an inability to store information temporarily.

Since grammar is a mechanism that relates sound to meaning, many grammatical differences will necessarily correlate with differences in meaning, so attempts to tie Broca's area to grammar may also be confounded by the cognitive demands of processing semantics. For example, Thompson-Schill et al. (1997) argue that generalized "selection demands" increase in complex sentences, potentially confounding the signal from grammatical processing. In three tasks (generating a verb semantically associated with a presented noun, judging the consistency of a picture and a word, and judging the semantic similarity of a word to a target), Thompson-Schill et al. (1997) varied the degree to which the response competed against alternatives. For example, producing a verb to go with *hand* requires selecting from a larger set of possibilities than producing a verb to go with *gun*. Broca's region was more active under higher selection demands, and crucially was not activated by a task with low selection demands. They conclude that the inferior frontal gyrus (IFG, which contains Broca's area) is involved in selecting from among semantically specified items, though not in simply retrieving them or in grammatical processing *per se*.

The potential confound between syntactic complexity and semantic selection is difficult to eliminate even from studies that are carefully designed to focus on syntax. Using functional magnetic resonance imaging (fMRI), Embick et al. (2000) compared brain activity when subjects detected words that were misplaced in a sentence (e.g., *John drove to store the in a very fast car two weeks ago*), which presumably engages syntactic processing, with activity when the subjects detected words that were merely misspelled (*John drove to the store in a very fasvt car two weeks ago*), which

involves only orthographic and phonological processing. Classic language areas were active in both conditions, but the greatest difference was seen in Broca's area, leading the authors to conclude "that Broca's area is specifically involved in syntactic processing". Yet it is still possible that only the sentences with syntactic anomalies trigger the listener to re-analyze the sentence, a process that may involve assuring that the revised sentence is consistent with a specific interpretation, thus activating the semantic system as well.

Yet another potential confound is articulation (Wise et al., 1999) and articulatory planning (Dronkers, 1996), long associated with Broca's area on both anatomical grounds (proximity to the mouth and face region of the motor cortex) and aphasiological evidence (since dysarthria and dyspraxia of speech are common symptoms in the family of syndromes known as Broca's aphasia). It was specifically to avoid contamination of grammatically induced activity in Broca's area by sub-vocal rehearsal (Smith et al., 1998) that Caplan et al. (2000) had subjects repeat an unrelated word during their sentence comprehension task, with some danger of altering subjects' normal mode of language processing.

Syntax versus Morphology as a Domain for Studying the Neural Bases of Grammatical Processing

We suggest that many of the problems in assigning language functions to brain areas come from the focus on syntax, especially in the neuroimaging experiments. Syntax is not the only component of combinatorial grammar. Traditionally grammar is divided into syntax, the combination of words into phrases and of phrases into sentences, and morphology, the combination of morphemes and simple words into complex words. Morphology in turn is often divided into derivation, which generates new words (*learn + -able → learnable*; *mice + bait → mice-bait*), and inflection, which modifies a word according to its role in a sentence or discourse context (*walk + -ed → walked*; *hawk + -s → hawks*). These processes are, like syntax, highly productive; indeed, in many languages they show greater complexity than syntax. In Turkish, for example, each verb comes in millions of inflectional forms, and rules must be attributed to speakers to circumvent the combinatorial explosion of memory entries and learning episodes that would be required by sheer memorization. In languages with complex morphology, syntax often plays a subsidiary role, and speakers have considerable freedom in ordering words, with thematic relations conveyed mostly by inflections for case and agreement.

Though most studies of the neural bases of grammar have examined syntax, there may be advantages to examining morphology. Whereas syntax involves relationships across words, which are spread out in time, often by several seconds, morphology takes place within a single word, often a single syllable, and therefore places few of the demands on working memory that have confounded neuroimaging studies of syntax. The semantics of inflectional morphology can also be relatively simple, sometimes involving the addition of a single semantic feature such as "plural" or "past-tense". The grammatical component of an act of morphological processing can be isolated relatively cleanly from the input-output components (such as recognizing and retrieving a word, preparing it for articulation, and articulating it) by comparing the task of inflecting a word (e.g., seeing *walk* and saying *walked*) with the task of repeating it verbatim (e.g., seeing *walk* and saying *walk*).

The inflectional process can be further subdivided into two component subprocesses, sometimes called morphosyntax and morphophonology. The first is the manipulation of features such as tense, person, number, and gender, generally in response to demands by syntax, as when a clause is obligatorily tensed (compare, e.g., *I want him to leave/*that he left* and *I think that he left/*him to leave*), or when a subject must agree with a verb. The second is encoding such features into audible phonological signals. The difference between these subprocesses is made clear in cases of zero-morphology. For instance, an English verb stem (e.g., *walk*) is not modified by the addition of a suffix in the present tense for first and second persons and for third person plurals (*I, you, we, they walk*). Knowing that such an unmarked form is called for by these combinations of tense, number, and person is part of morphosyntax, and involves only the manipulation of abstract features, with no phonological consequences. Knowing that suffixed forms are called for in the past tense (*walked*) and third person singular present tense (*walks*) involves both the manipulation of morphosyntactic features and, in addition, the execution of a process that appends the suffix *-ed* or *-s* to the stem.

A final advantage in using inflectional morphology to dissect grammatical processing is that the morphophonological process can in turn be dissected into two distinct kinds of cognitive operations. With regular forms, such as *walk – walked* and *hawk – hawks*, a suffix is predictably applied to the stem. This may be done even with novel stems, as in neologisms like *spammed* and *moshed*, which people readily inflect even if they had not heard the verb in the company of that suffix before and hence could not have memorized the past-tense form. With irregular verbs, in contrast, such as *bring – brought, ring – rang*, and *fling – flung*, no consistent phonological change is applied, and the inflected form must be retrieved from lexical memory. Under the assumption that regular forms generally require the concatenation of morphemes in real time, whereas irregular forms

require lookup from memory (the 'words and rules' theory; Pinker, 1991, 1999; Pinker and Ullman, 2002), a comparison of the two can reveal the respective neural substrates of grammatical combination and lexical lookup. Alternatively, there are theories that attribute both regular and irregular inflection to a single process, either computation by a battery of rules (including minor rules that generate irregular patterns such as *-ing* → *-ung*; Halle and Mohanan, 1985; Chomsky and Halle, 1968/1991; Albright and Hayes, 2003) or lookup from a connectionist associative memory (Rumelhart and McClelland, 1986; Joanisse and Seidenberg, 1999; McClelland and Patterson, 2002). A failure to find any difference in the neural substrates of regular and irregular inflection would be consistent with such single-mechanism alternatives.

As mentioned, inflectional errors are some of the longest-documented and most apparent deficits in Broca's aphasics (Dronkers et al., 2000; Goodglass, 1973; Friedmann and Grodzinsky, 1997), but there have been few neuroimaging studies focusing on inflectional morphology, especially in production (other than a few, reviewed below, that compare regular to irregular inflection). In this study we use the relatively tractable but still combinatorial system of inflectional morphology to investigate the neural substrates of abstract grammatical processing, and the possible role of Broca's area in such processing. Subjects read words on a screen and either repeated them verbatim or inflected them for tense or number, while brain activity was recorded with fMRI. The simple task spares subjects from having to hold words of different lengths in working memory, and since the item being manipulated is a single word, one can control for low-level features such as length, syllables, frequency, pronounceability, and concreteness, in a way that would be prohibitive for an entire sentence.

Different conditions potentially can isolate the neuropsychological components involved in an act of grammatical processing. When people read a word and repeat it verbatim, the minimum processes include reading and recognizing the word, looking up its phonological representation, preparing it for articulation, and articulating it. When people inflect a word in the third person plural or another context calling for a zero-marked form (e.g., they see *walk* in the context 'Everyday they ….' and say 'walk'), they must do all these things and also determine that the linguistic context calls for leaving the form unchanged, a simple instance of morphosyntactic processing. When people inflect a word in the past tense (e.g., they see *walk* in the context 'Yesterday they…' and say 'walked'), they must do all the components of both tasks previously described and, in addition, execute some operation that results in a phonologically different output: under the words-and-rules theory,

either looking up the past-tense suffix and concatenating it to the verb stem (for regular verbs) or retrieving a distinct form (for irregular verbs).

Under the simplest assumption of how psycholinguistic processes, characterized in information-processing terms, map onto patterns of neural activity, we might expect the pattern of neural activity recorded for repeating a word to be a subset of the activity for producing a zero-inflected form, the difference indicating the neural substrates of the computation of morphosyntactic features. Similarly, we might expect the neural activity for uttering a zero-marked form to be a subset of the activity recorded for uttering an overtly inflected form, the difference indicating the neural substrates of morphophonological manipulation. We note that these assumptions correspond to the "pure insertion" model of how information processing components are combined, viz., that a given component operates in the same way, and has the same distribution in the brain, regardless of which other components accompany it in a given task. That assumption may or may not be true in any given case, but it can be addressed in part by testing whether the patterns of activity recorded in the present tasks really do exhibit a subset-superset relationship, as opposed to being disjoint or overlapping.

Regular and Irregular Inflectional Morphology

What are the predictions about the effects of the regular/irregular contrast? According to the words-and-rules theory, irregular forms (and any regular forms or parts thereof that are dependent on memory storage) should be tied to the neural substrate for lexical memory, which is often thought to be concentrated in temporal and temporoparietal regions (Damasio, 2000; Goodglass, 1993; Martin et al., 1996). Regular forms (especially those for low-frequency and novel words) should be tied to the substrate for grammatical combination, traditionally associated with circuits which include Broca's area, other regions in the prefrontal cortex (PFC), and the basal ganglia (Ullman et al., 1997; Dronkers et al., 2000; Damasio, 1992). Many neuropsychological studies are consistent with this assignment. Patients with anomia following damage to left temporal/parietal regions are (compared to control patients) worse at producing irregular than regular verbs, produce regularization errors like *swimmed* (which occur when no memorized form comes to mind and the rule applies as the default), and are relatively unimpaired at generating novel regular forms like *plammed* (Ullman et al., 1997, 2005; Tyler et al., 2002a; Miozzo, 2003; Shapiro and Caramazza, 2003). Patients with agrammatism following damage to left frontal perisylvian regions show the opposite pattern: more trouble inflecting regular than irregular verbs, a lack of errors like

swimmed, and difficulty suffixing novel words (Ullman et al., 1997, 2005). Other evidence linking anterior cortex with regular inflection and posterior cortex with irregular inflection comes from studies of inflectional priming in patients with brain damage (Tyler et al., 2002b; Marslen-Wilson and Tyler, 1997, 1998) and of event-related potentials (ERPs) in healthy speakers (Munte et al., 1999; Gross et al., 1998; Penke et al., 1997; Weyerts et al., 1997).

Involvement of the basal ganglia in regular inflection is suggested by the finding that Parkinson's disease patients have more difficulty inflecting regular and novel verbs than irregular verbs, and seldom make overregularization errors (Ullman et al., 1997; Ullman et al., 2005). In addition, Tsapkini et al. (2001) describe a Greek-speaking patient with basal ganglia damage who performed perfectly on Greek irregular past-tense forms but performed significantly worse with regular forms (he performed worst of all on forms that combined a regular suffix with an irregular stem change).

Penke and Krause (1999), testing noun inflection in a sample of German-speaking Broca's patients (lesions unspecified), report that most found the regular plurals more difficult [consistent with the pattern of Ullman et al. (1997) and other previous studies], but one showed the opposite dissociation. The recalcitrant pattern shown by this last patient was seen even more pervasively by Penke et al. (1999) in a study with a similar patient sample. Though they replicated the dissociation of regular and irregular forms, in this study the majority of patients did not display the usual linkage between regular processing and Broca's aphasia: most of their patients had trouble inflecting *irregular* verbs, and often overapplied the regular suffix to them, but had little or no trouble inflecting regular verbs.

Neuroimaging studies on the regular-irregular distinction present a still more complicated picture (Jaeger et al., 1996; Sach et al., 2004; Rhee, 2001; Rhee et al., 2003; Beretta et al., 2003; Dhond et al., 2003). All such studies show different patterns of activity when subjects inflect irregular and regular forms, consistent with the prediction of the words-and-rules theory that the two processes have different sets of neural substrates. In particular, all show greater overall activation for irregular than regular forms, and all show regular inflection to be more left-lateralized and irregular inflection to be more bilateral (consistent with much neuropsychological evidence that the lexicon is less lateralized than grammatical combination). Unfortunately, the respective areas associated with regular and irregular inflection differ from study to study, possibly because of methodological differences: some used PET, others fMRI; some used English, others German; some compared regular and irregular inflection directly, others first subtracted out activity during verbatim repetition of the stem. Some (Sach et al., 2004; Jaeger et al., 1996) used blocked designs in which subjects inflected regular and irregular forms in different blocks of trials, which may induce subjects to use different conscious strategies for the two kinds of verbs (Seidenberg and Hoeffner, 1998). Moreover, there is little to no evidence that the regular-irregular distinction correlates with differences in functional neuroimaging activity between frontal and temporal-parietal regions. If anything, the studies show increased activity in left frontal regions for the *irregulars*.

There are numerous possible explanations for the discrepancy between the neuroimaging data on the one hand and most of the neuropsychological and electroencephalographic data on the other. Neuroimaging studies identify the set of regions recruited in normal function, whereas lesion studies index single regions that are so *necessary* for a given function that the function is grossly compromised by the lesion. Moreover, there are many reasons to expect that in normal functioning, the regular-irregular distinction does not map perfectly onto a neural distinction between grammatical computation and lexical lookup. First, both regular and irregular forms require the processing of morphosyntactic features such as "past tense" and "plural", which originate in the syntactic representation of the sentence or in the speaker's intentions and trigger a call for a specific inflected form; the difference is only in which of the two kinds of processes succeeds in supplying the form. Second, if, as seems likely, regular and irregular processes are activated in a parallel race fashion (Baayen et al., 2002; Pinker, 1999; Caramazza et al., 1988), both processes may operate for both kinds of forms, the difference lying only in which one terminates and which one runs to completion. Third, a strict dichotomy between whole regular and whole irregular forms may not always be appropriate. Some complex words may consist of an irregular stem with a regular suffix; this is common in languages other than English (Berent et al., 2002) and may be found in some English plurals such as *leaf-leaves* and *house-houses* (see Senghas et al., 2005). Fourth, certain regular forms may be stored in memory, diluting any difference from irregulars in average neural activity, if they are high in frequency, higher in frequency than their stems, phonologically similar to irregulars, inflected with an affix which is homophonous with some other affix, or in alternation with an irregular variant (Pinker, 1999; Baayen et al., 2002; Hay, 2001; Alegre and Gordon, 1999; Ullman, 1999). Fifth, even when they are computed in real time, regular forms may require at least two cycles of memory lookup, one for the phonology of the stem, another for the phonology of the past tense suffix *-ed*; irregular forms differ only in requiring secondary

lookup of a form that is more phonologically and semantically substantial and less overlearned than the regular suffix. Sixth, irregular verbs, for their part, may require not just activation of the lexicon but the control processes that guide access to the lexicon (often linked to frontal regions such as Brodmann's area 47 and other regions of lateral PFC) (Kerns et al., 2004b). These control processes must send out a search query for the form with an intersecting specification of the lexical item and the inflectional feature (e.g., *to bring* ∩ past-tense), while inhibiting partial or false matches from overlapping memory items (e.g., for *brought*, interference from *drank* and *sprung*). Seventh, irregular inflection requires not just retrieval of the irregular form but suppression or "blocking" of the regular rule, to prevent overregularizations such as *bringed* (Marcus et al., 1992; Pinker, 1999; Ullman, 1999). Though the neural substrates of blocking are unknown, they may overlap with cortical circuits that effect cognitive inhibition and control. These may include the anterior cingulate cortex (ACC), which has been implicated in the signaling of conflict situations, various regions of PFC, which resolve the conflict (Miller and Cohen, 2001; Kerns et al., 2004a), and regions dorsal to classic ACC such as medial supplementary motor area (SMA), which has been implicated in error and conflict signals in trials with fixed stimulus-response mappings (Holroyd et al., 2004).

All these considerations suggest that while there may be differences in the processing of regular and irregular forms for neuroimaging to reveal, they may not be restricted to a simple distinction between anterior and posterior regions, and that considerable design complexity may be needed to tease apart the component processes for each kind of inflection. The present study is a first step in this project: it uses an event-related (ER) rather than a blocked design (to minimize the use of ad hoc strategies for regular and irregular forms), examines the inflection of both nouns and verbs, and examines the regular-irregular difference in the context of a larger set of variables designed to identify the processing components that regulars and irregulars share in addition to the ones on which they differ.

Nouns versus Verbs

Another variable explored in the present study is the distinction between nouns and verbs, which bears on the extent to which grammatical processing is spatially localized or distributed in the brain. The failure to find any region that is consistently associated with grammatical processing had led to the hypothesis that such processing is widely distributed across the brain, perhaps taking place in the same regions in which the words being modified are stored, and thereby obliterating any principled distinction between lexicon and grammar in the

brain (e.g., Bates and Goodman, 1997). This hypothesis, loosely associated with connectionist approaches, would contrast with a more traditional box-and-arrow view in which words, regardless of where they are stored, are retrieved then shunted to a central grammatical processor for inflection or combination with other words. This can be examined by comparing the inflection of verbs and nouns.

It is controversial whether nouns and verbs have differing neural substrates, and if so, whether the differences come from grammatical category *per se* or from other features confounded with the categories. Caramazza and colleagues have found patients selectively impaired on verbs or on nouns, including non-words (Caramazza and Hillis, 1991; Shapiro and Caramazza, 2003), as well as selective disruption of verbs during transcranial magnetic stimulation (TMS) disruption of left inferior PFC (Shapiro et al., 2001; see also Cappa et al., 2002). They conclude that verbs are more concentrated in frontal neural regions, and nouns more concentrated in temporal-lobe regions (Caramazza and Shapiro, 2004). In contrast, Pulvermuller et al. (1996, 1999) have measured ERPs during reading and lexical decision of nouns and verbs, and while they found category differences in similar locations (nouns near visual areas and verbs near motor areas) they attribute the difference to statistical associations of verb semantics with motor actions and noun semantics with visualizable objects, based on the finding that when they presented action-related nouns or visualizable verbs, the differences went away (Pulvermuller et al., 1999; see also Luzzatti et al., 2002; and Bird et al., 2000, 2001). Neuroimaging studies have not resolved the debate. Perani et al. (1999) found noun-verb category differences with PET, which did not interact with concreteness, yet only found voxels more active for verbs, none more active for nouns, leaving it unclear whether the verbs involve qualitatively different systems from nouns or are just more demanding. In two noun-verb PET experiments (lexical decision and semantic categorization), Tyler et al. (2001) found extensive activation they interpret as a semantic network but found no differences as a function of word class.

In most of the studies of grammatical category, subjects process single words outside a grammatical context, such as single word repetition, picture naming, or lexical decision. This makes it unsurprising that the measurable difference between categories is often dominated by differences in meaning rather than abstract grammatical properties. Any difference in grammatical properties would be more likely to emerge in tasks that require the use of nouns and verbs in their differing grammatical contexts. A task that compares the process of inflecting nouns and verbs according to their linguistic context with the process of repeating a word may help to

specify whether nouns and verbs differ in storage, grammatical processing, or both. If inflectional processing simply emerges from the network of associations stored with words, then the inflection of nouns and verbs should be co-localized with any separate storage areas for nouns and verbs. Indeed, a difference in the loci involved in the inflection of nouns and verbs might be found even if they are stored in the same locations: after being retrieved, they may be processed in different areas to prepare them for their different grammatical roles in the sentence. Alternatively, if there is a central grammatical processor that interfaces with the lexicon but is distinct from it, one should see a common set of loci activated for inflection, whether it is nouns being pluralized or verbs being inflected for tense, person, and number.

Only Shapiro et al. (2001), Shapiro and Caramazza (2003), and Tyler et al. (2004) employed a task involving inflection, and only Shapiro and Caramazza (2003) used a sentence context (rather than a metalinguistic task) to cue the inflection. The sole neuroimaging study of these, Tyler et al. (2004), was aligned with the present study in using inflection to clarify the differences and similarities in noun and verb processing. They replicated a previous PET study (Tyler et al., 2001), in which subjects saw triplets of uninflected nouns or verbs and pressed a button to designate whether the target word fit the other two semantically, and in which no noun-verb differences were found. In the new study, using fMRI, the words in each triplet were regularly inflected; this time they found greater verb than noun activation in left inferior frontal gyrus (LIFG) including Broca's area, no regions with greater noun than verb activation, and no noun-verb differences in temporal lobes. The LIFG region, when compared individually to a baseline condition, was active for both nouns and verbs, and they interpret stronger activity for verbs in terms of greater contribution of verb than noun morphology to grammatical structure. These results provide some evidence against the hypothesis that words are inflected where they are stored. The LIFG was the region in which inflection-related activity was concentrated, and was the only region showing differences in activity between nouns and verbs; no such difference was found in the temporal lobes, which have generally been considered the seat of lexical storage. The present study goes beyond Tyler et al. (2004) by examining production instead of recognition and by directly comparing noun-verb differences in tasks that require inflection and tasks that do not.

The present study, then, seeks to identify the neural substrates of grammar in the abstract sense in which linguists characterize it, rather than aspects of linguistic processing that are reducible to working memory, semantics, phonology, or lexical knowledge. Specifically, the current design tests whether there are brain regions that are active in inflectional morphology regardless of whether the inflectional modification is phonologically overt or silent (*They walked vs. They walk*), whether it requires a predictable suffix or an unpredictable vowel change (*walked vs. came*), whether it involves a verb or a noun (*walked vs. hawks*), and with minimal demands on working memory and semantic selection.

METHOD

Subjects

Eighteen healthy, right-handed native English speakers (7 female, 11 male) gave written consent and were paid to participate. Their mean age was 20.6 years, with a range of 18 to 25. Subjects were excluded if they had participated in more than five previous fMRI studies or an earlier version of this study, or if they met any of the standard exclusion criteria for fMRI. Participation was covered by Institutional Review Board approval, and data were treated according to the privacy guidelines of the USA Health Insurance Portability and Accountability Act.

Task

The experiment employed a cued covert production task, schematized in Figure 1. The cue was a short context frame specifying a particular inflection, e.g. "*Yesterday they ___*" which calls for a past tense verb. The context frames allowed us to cue a different inflection on each trial without forcing subjects to think about metalinguistic categories such as "past tense" or to memorize arbitrary visual cues. In all cases the context frame was followed by a target word, which appeared in a small phrase with the marker *to* (for verbs) or *a/an* (for nouns). The task was to produce silently the form of the target word that would fit into the blank (e.g., in response to *Yesterday they ___ …to walk*, the subject would silently think 'walked'), and then press a button. The button press was intended to keep the subject alert, to warn the experimenter of waning attention or sleep, and to provide a reliable benchmark activation (in contralateral motor cortex, hand area) to compare with activations related to this new cognitive task. Subjects used only the left hand to press the button, so this activity would not be confounded with any language-related motor activity in the left hemisphere. Since the silent task provided no indication of response accuracy, and since during the practice sessions subjects were observed to differ in their tendency to press the button simultaneously with saying the word or only after completing it, button-press latencies were not deemed a reliable measure of reaction time and are
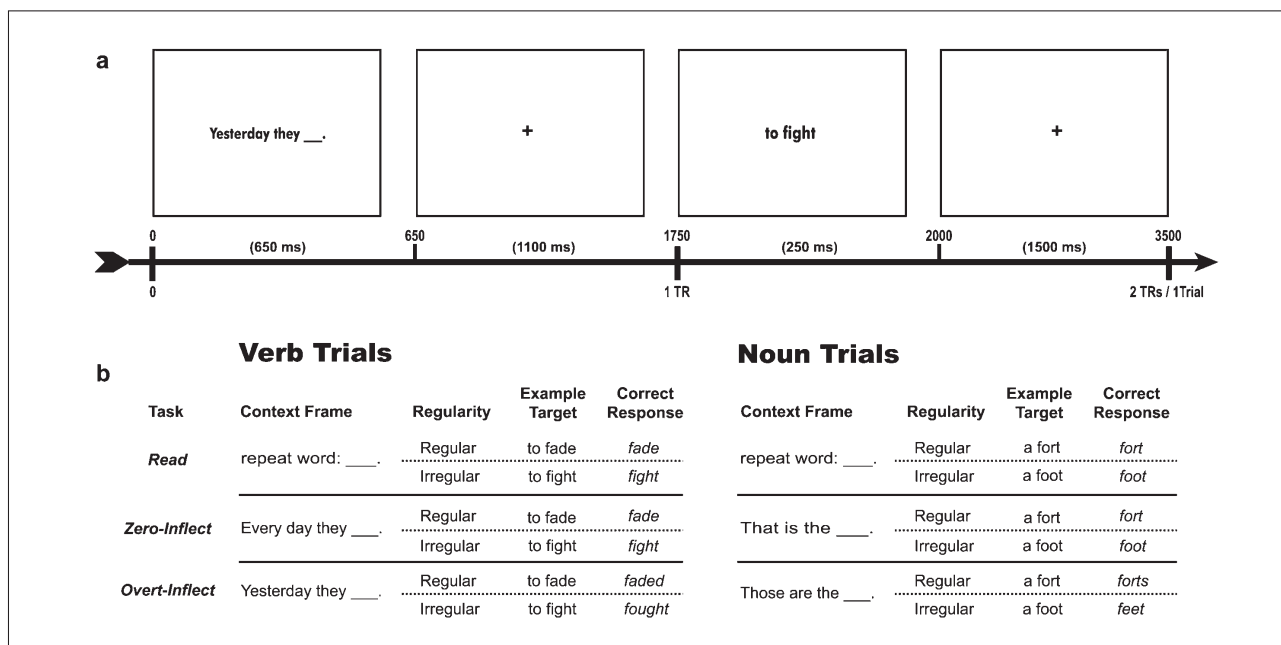
Fig. 1 – *Summary of experimental conditions. (a) Timeline and what was shown on screen, for a single example trial, (b) Examples of each experimental condition.*

not reported. The marker (*to* or *a/an*) was included to inhibit a strategy of simply concatenating the target word to the context frame, which would work for two thirds of the trials (Zero-Inflect and Read) while on the other trials (e.g., **Those are the ___ ...hawk)* could cause the subjects to experience an anomaly response (which strongly affects fMRI signals). Since the markers are presented on all trials, their effects should disappear in subtractions of one condition from another.

Design

The experiment had a 2 × 2 × 3 factorial design: Grammatical Category (Noun/Verb), Regularity (Regular/Irregular) and Task (Overt-Inflect/Zero-Inflect/Read). For verbs, the Overt-Inflect condition corresponded to the frame *Yesterday they ___*, which calls for a past-tense form, either one with the regular suffix *-ed* or an irregular form. The Zero-Inflect condition corresponded to the frame *Every day they ___*, which calls for the third person plural present tense, which in English has no phonologically overt marking (some linguistic theories posit a silent 'zero morpheme' to preserve the idea that all inflected forms are suffixed). The Read task corresponded to the frame *read word:___*. For nouns, the Overt-Inflect condition corresponded to the frame *Those are the ___*, which calls for a plural form, either one with the regular suffix *-s* or an irregular form. The Zero-Inflect condition corresponded to the frame *That is the ___*, calling for a singular noun, which in English has no phonologically overt marking. For examples of each condition, see Figure 1.

Subjects saw each word only in one of the three tasks (Overt-Inflect, Zero-Inflect, or Read). The assignment of words to tasks was random but consistent across subjects. The sequence of trials was broken into three runs, each lasting 6 min and 25 sec. To increase the number of trials and hence signal quality, the entire paradigm (i.e., the three runs) was repeated three times. The order of the runs was varied across the repetitions for a given subject, and differed for the different subjects. However, the order of trials within a given run was constant across subjects.

Materials

One hundred twenty English nouns and 120 English verbs were used as targets, 60 each with regular and irregular forms. Stimuli were selected according to a semi-automated procedure to implement several criteria simultaneously (Sahin, 2003).

A database was created using Microsoft Access, incorporating raw frequency numbers from the AP newswire corpus (see Church and Hanks, 1991), frequency and word length values from the Brown corpus (Francis and Kucera, 1982), syllable counts and subjective ratings from MRC-2 linguistic database (Coltheart, 1981), including norms of imageability and familiarity (Paivio et al., 1968). The database incorporated frequency values for the inflected form and for the stem cluster (stem plus all inflected forms).

In English there are far fewer irregular words than regular ones, and far fewer irregular nouns than irregular verbs. Therefore the limiting factor was the availability of irregular nouns, so they were used as the starting point. The English language makes this especially problematic because

only a handful of common irregular plurals undergo some stem change (*men, women, children, feet, teeth, mice,* and *geese*). These are too few to yield interpretable fMRI data alone, so they were supplemented by somewhat more problematic kinds of irregular plural, including compounds (e.g., *grandchildren*), no-change (e.g., *sheep – sheep*), Latin (*nucleus – nuclei*), Greek (*phenomenon – phenomena*), and regressive-voicing fricatives (*wolf – wolves*). Senghas et al. (2005) present evidence that English speakers treat borrowed Latin and Greek plurals as irregular, at least in how they treat them with regard to other grammatical processes such as compounding. However, it is possible that at least some speakers apply special suffix-changing rules to generate them, which would mean that they were processed as regulars, not irregulars. In addition, Senghas et al. (2005) show that English speakers treat regressive-voicing plurals as hybrids consisting of an irregular stem (e.g., *wolv-*) subjected to regular suffixation. These unavoidable problems decrease the likelihood of finding a regular-irregular difference in the fMRI data for the nouns.

Selection and matching were accomplished in multiple passes. To exclude nouns that were easy to misread as verbs and vice-versa, most noun-verb homographs were eliminated. Also, words with both regular and irregular variants and words with extreme frequencies were eliminated. An algorithm then selected, for each irregular noun, the irregular verbs that best matched it on a number of weighted criteria. It attempted to achieve matches of 90% or greater for each of the variables in the database, while giving greater weight to Brown-corpus form frequencies and stem-cluster frequencies than to the AP frequencies, and greater weight to number of syllables than to raw length. The process was iterated, first for those irregulars that had values in the database for the Paivio norms, then the rest, until both Irregular lists were set. Next, the algorithm iteratively selected regular forms for each irregular, aiming for phonological similarity when possible (e.g., *wolves/valves, parentheses/democracies, crept/cropped, bound/downed*).

The result of this process was a set of item lists whose mean log frequencies for the major variables were mostly matched (no statistically significant differences), except for a greater average Francis-Kucera (1982) inflected-form frequency of the Irregular compared to Regular Noun plurals, a greater average length for noun *versus* verb irregulars, and a lower average frequency for nouns than verbs (a consequence of including Greek and Latin plurals and their matched regulars).

Procedure

Presentation of the experimental materials was controlled by Presentation® software (Neuro-Behavioral Systems), version 0.5. Context frames were presented on a screen as image files, adjusted to be identical in horizontal length and to subtend a visual extent on screen small enough to allow subjects to view them without scanning away from the center.

The experiment used a rapid ER paradigm (Buckner, 1998; Burock et al., 1998), and included all trial types in all runs in a pseudo-random order. Stimulus presentation was jittered in time to allow deconvolution of the event-related functional magnetic resonance imaging (ER-fMRI) signal, according to a schedule optimized by the "optseq" tool of the FreeSurfer-Functional Analysis Stream (FS-FAST) fMRI analysis toolkit (Dale, 1999). The inter-trial intervals totaled 27% of the experiment duration (optimized; see Sahin, 2003), and the blood oxygenation level-dependent (BOLD) signal during this time was analyzed as the "Fixation" baseline.

Immediately before the scan, subjects received a schematic demonstration of the task on flash cards and then practiced by performing the equivalent of a full run of the task (with words not on the actual stimulus list) on a standalone computer workstation. They first spoke the correct responses out loud until the experimenter was satisfied they understood the task, then silently produced the rest while the experimenter observed the button presses. Pilot testing had revealed that people can interpret the *Every day they* ___ frame as consistent with the past tense (e.g., *Every day they walked*), so the experimenter emphasized that the present tense was intended. Subjects reported no trouble complying with this instruction.

fMRI Data Acquisition

MRI data were collected on a Siemens Magnetom Trio 3-Tesla whole-body system. BOLD contrast was obtained with a gradient-echo echo-planar imaging (EPI) sequence [TR = 1750 msec; TE = 30 msec; flip angle = 90; FOV = 200 mm; base matrix = 64 × 64 (3.125 × 3.125 mm)]. Twenty-five axial 5.0 mm slices (skip .5 mm) were collected to cover the brain, except, in some cases, the cerebellum. High-resolution structural images, for functional underlay and group co-registration and averaging, were collected with a three-dimensional magnetization prepared rapid gradient echo (MPRAGE) protocol, at 1.0 × 1.0 × 1.33 mm resolution.

Projection of stimuli on the scanner screen (from the rear) was synchronized with millisecond precision to a TTL pulse from the scanner, preventing the experimental presentation from drifting in time relative to the scanner.

fMRI Data Analysis

fMRI data processing was carried out using FS and FS-FAST software packages from the Massachusetts General Hospital Athinoula A.

Martinos Center for Biomedical Imaging, and Cortechs Labs, LLC (Charlestown, MA, USA).

The T1-weighed structural images were processed through FS to reconstruct the cortical surfaces (Dale et al., 1999; Fischl et al., 1999a, 2001). These surfaces were then registered with a surface-based atlas (Fischl et al., 1999b). Functional (EPI) data sets were motion-corrected using analysis of functional neuroimages (AFNI) (Cox, 1996), spatially smoothed with a 7 mm full-width half-max (FWHM) Gaussian kernel, and intensity normalized (over time and space) to a grand mean value of 1000. The functional volume of each subject was registered to the structural (T1) volume for that subject in order to align the activation maps with the cortical surface. The hemodynamic response function (HRF) was modeled using a gamma-variate function (similar to the SPM canonical HRF) with a delay of 2.25 sec and a dispersion of 1.25 sec (Dale and Buckner, 1997). The HRF amplitude for each event type was estimated at each voxel using a general linear model (GLM). Autocorrelation in the fMRI noise was accounted for by pre-whitening with a filter estimated from the residual autocorrelation function averaged over all brain voxels (Burock and Dale, 2000). Low-frequency drift was removed by including a 5th order polynomial in the GLM. Contrasts were computed as linear combinations of the HRF amplitudes (i.e., regression coefficients). These contrasts were then resampled to a computed surface space common to all subjects ('spherical space' – an alternative to Talairach space). Data were combined across all 18 subjects within this spherical space, using a random-effects analysis (with subject as a random effect), and smoothed in forty iterative steps with a surface-constrained smoothing algorithm.

Results were then back-propagated through the spherical-normalization transformation matrix and visualized on the reconstructed surface anatomy of one representative study subject in order to associate the BOLD activations with recognizable anatomical landmarks. The significance values for each surface-intersecting voxel were displayed as false-color overlay on the anatomy, in red-yellow scale for the positive tail of the contrast, and blue-light-blue for the negative tail.

Correction for multiple comparisons was carried out using the false discovery rate (FDR) technique (see Genovese et al., 2002). A global region-of-interest (ROI) was selected to include all voxels that were significant at the .001 level (voxel-wise) in an omnibus contrast (i.e., all tasks *vs.* fixation). The voxel-wise corrected threshold for each contrast-of-interest (COI) was chosen to achieve an FDR of .05 within all voxels of the global ROI for data included in that COI. This means that no more than 5% of the voxels ruled "active" in each contrast were in fact noise. Note that constraining the ROI based on the omnibus activation does not

bias the findings for the COIs; that is, it does not make it more or less easy to find false positives for a given COI, since the data for the COI are compared against all voxels active in the experiment. Similarly, the significance threshold used to select the global ROI does not bias the findings for the COIs.

RESULTS AND DISCUSSION

Overall Pattern of Activation in the Linguistic Tasks

Given the complex and often inconsistent patterns of activation seen in previous neuroimaging studies of inflection, we begin by comparing the distribution of neural activity during all task conditions to the Fixation condition (used as a low baseline) to see if the overall pattern is intelligible in light of existing knowledge of language and the brain. The pattern (Figure 2) fits well with classical models of the organization of language functions in the brain (Geschwind, 1979; Dronkers et al., 2000; Damasio, 1992). We observe bilateral activation in primary visual cortex (low-level perception of the visual stimuli), left-lateralized posterior inferior temporal regions [recognition of visual word forms (Dehaene et al., 2002; McCandliss et al., 2003; Cohen and Dehaene, 2004)], left posterior superior temporal cortex (Wernicke's area: retrieval of words' phonological representations), left Broca's area and surrounding inferior PFC (planning of articulation, grammatical computation, or both), left premotor cortex near the areas for the articulators [planning of articulation and possibly other functions (Wise et al., 1999; Toni et al., 2002)], and right motor cortex (hand area for the left-hand button press). Independent contrasts for each of the three task conditions against fixation (not shown) yielded similar activations. These patterns do not isolate grammatical computation or other components of linguistic processing, but they confirm that the present task yields an intelligible signature which makes contact with the literature and adds confidence to the interpretations of fine-grained contrasts among the conditions. Two other activated regions are less expected from the classic aphasiological literature but have a strong precedent in language neuroimaging. The first is a medial region (more pronounced on the left side) including the medial SMA and ACC. This is a frequently observed language task region (Turkeltaub et al., 2002) which may be involved in the initiation and suppression of articulation, especially in the context of selecting an appropriate response (Kerns et al., 2004a, 2004b). Also observed is activation in the left intraparietal sulcus, possibly involved in visual attention to the stimuli (Jovicich et al., 2001; Wojciulik and Kanwisher, 1999).
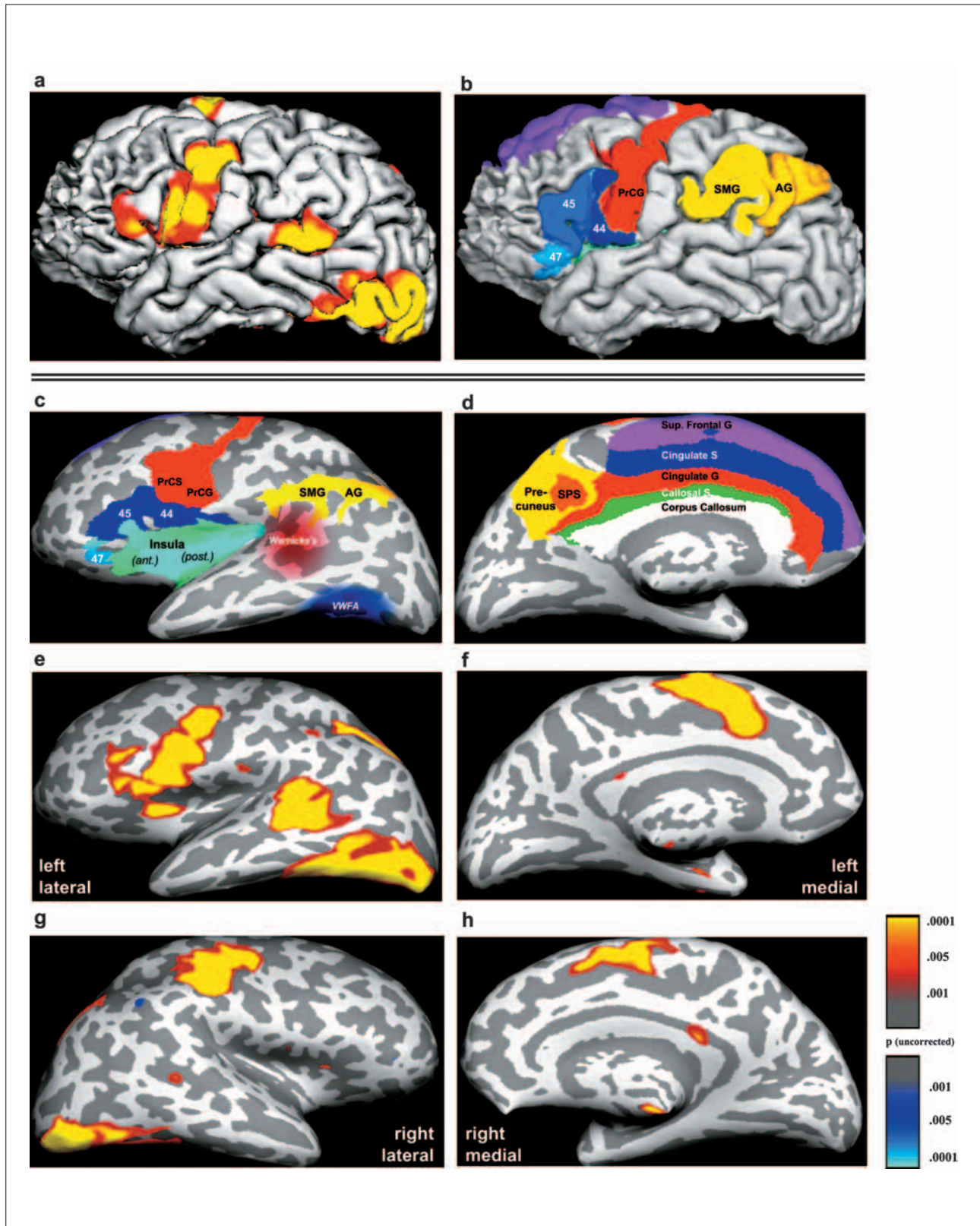
Fig. 2 – *Cortical regions more active during task conditions than visual fixation baseline (omnibus contrast). Maps indicate results of 18-subject, random-effects analysis, depicted on the brain of one of the subjects. Thresholded here at p < .001, with major clusters surviving a test at p < 10⁻⁶. All figures in this paper use inflated-surface representations of the cortex except (a) and the corresponding legend (b), which are presented to show the alignment of the activation patterns with recognizable gyral anatomy. Legends for the inflated-cortex representations are shown in (c) (left lateral) and (d) (left medial). The all-tasks-versus-fixation comparison is shown on the inflated cortex in (e) and (f). Brodmann areas 44,45 and 47 as marked; precentral sulcus (PrCS) and gyrus (PrCG) are mostly premotor Area 6, while primary motor Area 4 is the most posterior portion of PrCG. Also labeled are supramarginal gyrus (SMG); angular gyrus (AG); subparietal sulcus (SPS). Wernicke's area has no consensual anatomical definition, and the Visual Word Form Area (VWFA) is a recently posited functional area; their locations are shown approximately. Right hemisphere maps (g) and (h) show mild bilaterality of medial and primary visual activations, and motor activation for the left-handed button press. Voxels activated in this contrast formed the global ROI that was used to compute the False Discover Rate (FDR) corrected threshold for each orthogonal task-task contrast of interest (COI).*
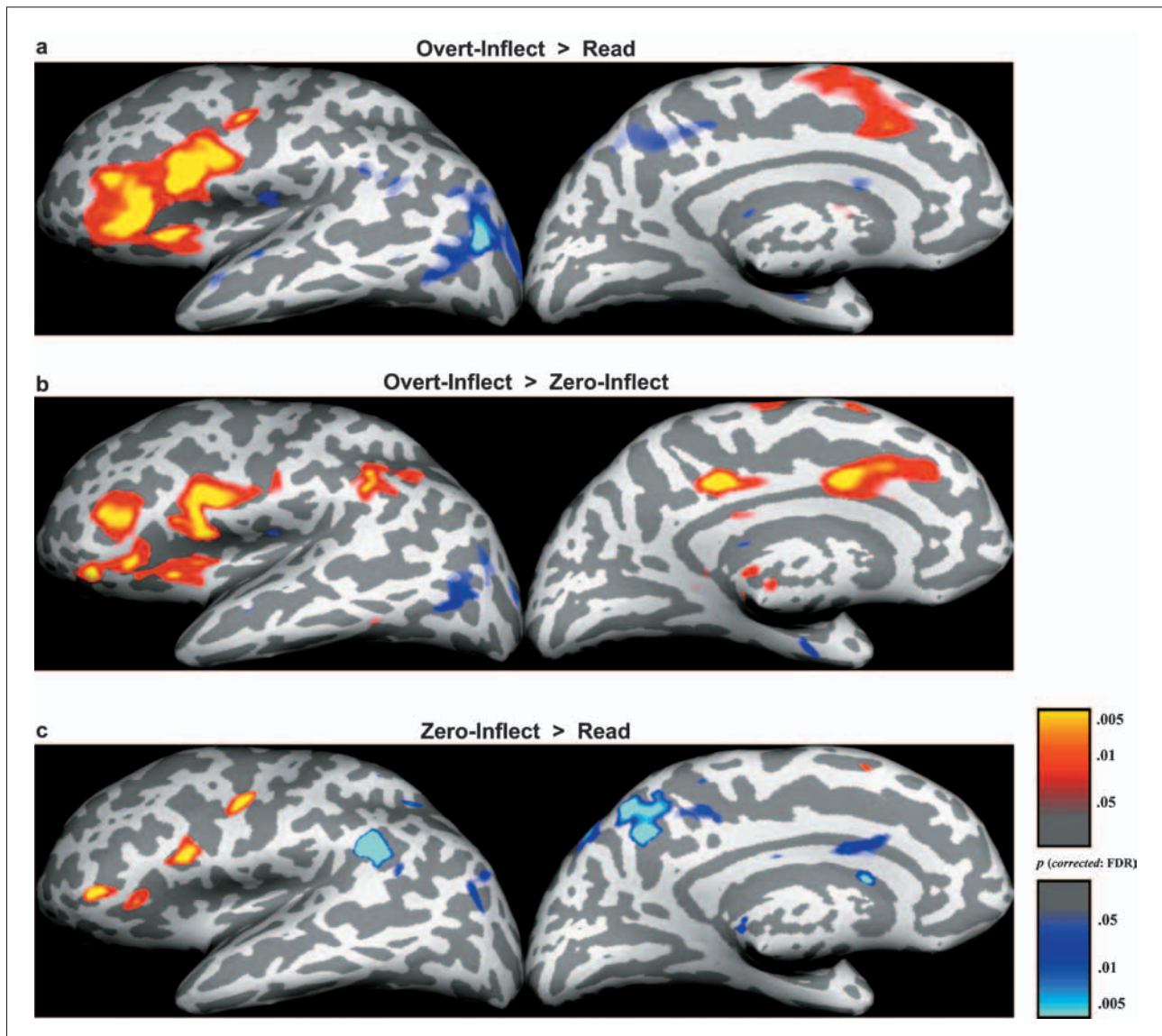
Fig. 3 – *Contrasts by inflectional task, aimed at partitioning inflection into its components. Thresholded at p < .05, corrected, with major clusters surviving a test at p < .000005 uncorrected. (a) The contrast Overt-Inflect > Read reveals a frontal network for inflection including BA 44, 45, 47, anterior insula, and medial SMA (bordering anterior cingulate). (b) Overt-Inflect > Zero-Inflect, a tighter contrast aimed at morphophonological processing. Each component of the network is activated, plus activations of AG and posterior cingulate. (c) Zero-Inflect > Read, a contrast aimed at morphosyntactic processing. The contrast shows activity in distinct regions of BA 44 and 47, as well as a middle precentral gyrus premotor region, and no activity increase in insula or BA 45. The Read task (blue in a as well as c) elicits activity in the supramarginal gyrus cluster, middle lateral occipital, and medial precuneal and subparietal regions.*

Grammatical Inflection as a Sufficient Activator of Broca's Area

To home in on the neural systems metabolically active during the processing of inflectional morphology, we first contrasted fMRI activation during Overt-Inflect and Read trials (Figure 3a). This contrast, which averages over nouns and verbs and regular and irregular forms, should index most of the processes involved in grammatically inflecting English words, eliminating the more peripheral components of the task such as reading, recognizing, and preparing to articulate the word. Broca's area was strongly activated in this contrast, within a network including much of the IFG and the anterior insula. The anatomical location of Broca's area is not uniformly agreed upon but here

we will take it to mean Brodmann Areas 44 and 45, or the *pars opercularis* and *triangularis* of the IFG. The medial views indicate involvement of the SMA/cingulate region in inflection; its role will be discussed in subsequent comparisons, as will the relative deactivation, compared to the Read task, in occipital and temporal cortex, and the precuneus (the blue areas in Figures 3a and 3c).

One of the primary questions posed in the Introduction can therefore be answered, namely that grammatical inflection is indeed sufficient to activate Broca's area. As noted, the task did not involve syntactic movement or long-distance dependencies, and the two conditions contrasted did not vary in working memory demands, especially sentential working memory. The result challenges both the strong hypothesis that Broca's

area and surrounding regions are responsible only for a specific component of syntactic processing, such as maintaining traces, and the opposite but equally strong hypothesis that it has no specifically grammatical role at all but only mediates domain-general processing resources. At least one role of Broca's area appears to be the combinatorial grammatical processing required by inflectional morphology.

Decomposing Inflection

To decompose the overall activity pattern associated with inflection into patterns tied to morphophonology (the manipulation of the overt phonological content of an inflected form) and to morphosyntax (the selection and application of grammatical features), we first contrasted the metabolic activity for the Overt-Inflect trials with that for the Zero-Inflect trials (Figure 3b). Recall that these conditions were cued with similar context frames, and both specified a particular inflectional category; the main difference was that the form elicited by the Overt-Inflect task (plural or past-tense) displays an overt morphological change in English (suffixed or replaced), whereas the form elicited by Zero-Inflect trials is phonologically identical to the base form presented on the screen. This contrast should index the retrieval of the phonological content of the regular suffix or irregular form, the concatenation of the suffix with the stem and consequent phonological adjustments of the juncture (for regular forms), the generation of the novel phonetic material, and the readying for final articulatory output. These processes were shown to activate parts of the entire circuit discussed in the preceding section (note that this contrast includes half the number of trials used in the preceding one, and therefore is lower in statistical power). The results verify the involvement of Broca's area in inflectional morphology, particularly in the manipulation of the overt phonological material.

To determine if Broca's region is sensitive to manipulation of abstract grammatical features encoded by morphology in the absence of phonological changes, we then contrasted the Zero-Inflect task with the Read task. Subjects covertly produced phonologically identical responses in the two conditions, but in the Zero-Inflect condition they arrived at the response as a solution to the problem of finding the form that satisfied the set of grammatical features (tense, number, and person) specified by the linguistic context. Since the contrast does not vary articulatory output, the hypothesis that the only role for Broca's area in linguistic processing is the manipulation of phonological content (either as preparation for articulation or in working memory) would hypothesize no Broca's area activity in this contrast. In fact, Broca's area was significantly activated (Figure 3c).

One possible confound in this comparison is that the Zero-Inflect context frame is slightly longer than the Read frame and, when completed, yields a short sentence. It could be argued that the contrast between the two conditions includes some grammatical processing of this short sentence. However, subjects saw each context frame 120 times (not including practice), reading them became automatic, and subjects reported in debriefing that they had ceased reading the frames all the way through and relied on the first word, which was designed to uniquely identify the condition. Even if they had processed the full sentences in most of the Zero-Inflect trials, the syntax required no movement, little if any working memory difference, and little semantic content other than in the inflected word itself. The main difference between the conditions thus appears to be the manipulation of the inflectional features.

Though the areas identified by the Overt > Zero and Zero > Read contrasts (Figure 3b and 3c respectively) are both concentrated in the left inferior frontal cortex, they do not overlap: Overt > Zero yields significant activation differences in BA 44, 45, 47, the anterior insula, and medial SMA, whereas Zero > Read yields significant differences in a more anterior portion of BA 44, more superior portions of BA 47, and a BA 6 premotor region at the junction of the precentral and middle frontal gyri. The simplest interpretation is that the former set of areas is more responsible for the manipulation of morphophonological content and that the latter set of areas is more responsible for the manipulation of abstract morphosyntactic features. No doubt this is too simple, but at least one aspect of the contrast between contrasts may be interpretable in these terms. The activation of the insula in the Overt > Zero but not Zero > Read contrast implicates the insula in phonological manipulation. This is consistent with the analysis of a large sample of aphasic patients by Dronkers (1996), who discovered a perfect correlation between damage to the insula and a diagnosis of apraxia of speech (AOS), a difficulty in articulatory programming resulting in distortions of the target word such as "yawyer" for *lawyer* or "tornyadiyudder" for *tornado*. These findings are also consistent with those of Dogil et al. (2003) who showed increasing anterior insula activity for repeating syllables of increasing phonological complexity. The convergence of these three findings, however, is imperfect. First, Dronkers' lesion-overlap region (the precentral gyrus of the insula) is posterior to the region shown to be metabolically active by the current data and the Dogil (2003) study. One possibility is that the discrepancy is an artifact of the difference between neuroimaging and lesion methods, perhaps because of constraints on the latter imposed by cerebral vasculature (Sahin et al., 1998; Caviness et al., 2002). The second discrepancy is that Dogil et al.
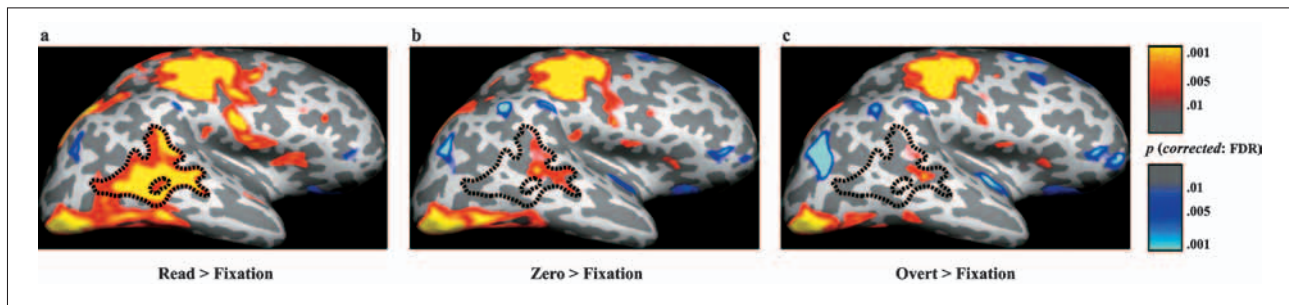
Fig. 4 – *Neural resources for the Read task are not a subset of networks for more inflectionally demanding tasks. (a) Right hemisphere activation for the Read > Fixation contrast (p < .01, corrected). The dotted line bounds activation clusters largely unshared by the zero-inflect (b) and overt-inflect (c) tasks.*

(2003) found insula activation only for overt, not covert, speech, leading them to suggest that the anterior insula is involved in the interface between symbolic phonological representations and motor implementation, rather than the manipulating of phonological representations (for a review see Ackermann and Riecker, 2004). It is possible that our task, designed to approach natural speech, evokes lower-level speech planning processes to a greater degree than Dogil's (2003) repeated syllables and words, or that insula activation for covert speech simply failed to reach significance in the Dogil (2003) study. The precise role of the insula in morphophonology, phonological programming, and phonetic implementation deserves attention in future research.

Reading Words versus Inflecting Words

A simple information-processing analysis of the Read-Word and Inflect-Word conditions might suggest that all the processes involved in reading a printed word aloud (a common baseline task in studies of morphology as well as semantics) would be included as a subset of the processes for inflecting the word. The fMRI contrasts between inflecting and reading words do not sit well with this analysis. There are several blue regions in Figures 3a and 3c), and since these contrasts subtract two similar conditions (not a task condition minus a baseline state), the deactivations are best interpreted as regions preferentially activated by the Read condition. In Figure 3a, which compares the Read task with the Overt-Inflect task, the Read trials are shown to recruit the middle and superior lateral occipital gyri and the supramarginal gyrus, with minor involvement of medial precuneus and subparietal regions. In Figure 3, which compares the Read task with the Zero-Inflect task, the Read trials are shown to recruit partially overlapping regions (strong SMG, medial precuneus, subparietal sulcus) as well as anterior cingulate. This suggests that the processes involved in reading a printed word aloud are not a simple subset of the processes involved in inflecting it. Further support comes from data on the right hemisphere, where the Read task appears to

activate extensive regions of the middle temporal gyrus and sulcus, superior temporal sulcus, and the homologue of Wernicke's area (Figure 4a). Furthermore the absence of significant activity in most of the temporal-lobe regions in Overt Inflect or Zero Inflect tasks relative to Fixation (Figure 4b and 4c) shows that the right-hemisphere regions are recruited specifically by the Read task rather than simply being recruited to a greater extent by this task than by other conditions.

Perhaps when people are cued that they merely have to pronounce a printed stimulus, they can adopt a strategy of attending closely to the visual word and mapping it onto its pronunciation in as direct a path possible (see Proverbio et al., 2004; Fiebach et al., 2002; and Joubert et al., 2004). This may explain why possible pathways between the secondary visual areas responsible for word recognition and the posterior perisylvian language areas involved in words' phonological representations appear to be differentially activated by the Read task. Given our poor understanding of the role of the right hemisphere in language processing (especially as indexed by neuroimaging), one can only speculate as to why there was such extensive right-hemisphere activation in the Read task. Possibly words (but not grammar) have a diffuse and redundant representation in the right hemisphere, which is ordinarily suppressed when grammatical processing is engaged, but can play a role in word recognition when the task demands are shallower, such as reading aloud (Baynes et al., 1992, 1998).

Recent work contrasting internally and externally focused brain activity may also bear on these results. Though baseline tasks are designed to keep the brain uniformly "quiet" or (more likely) uniformly noisy, many fMRI studies show puzzling "deactivations" relative to these baseline tasks in medial structures such as the precuneus and posterior cingulate. Raichle et al. (2001) specifically targeted the brain's resting state by scanning with PET while subjects lay awake with their eyes closed. They suggest that these midline areas are involved in actively maintaining a default mode (in which sensory information is monitored and evaluated for salience), and that they are actively
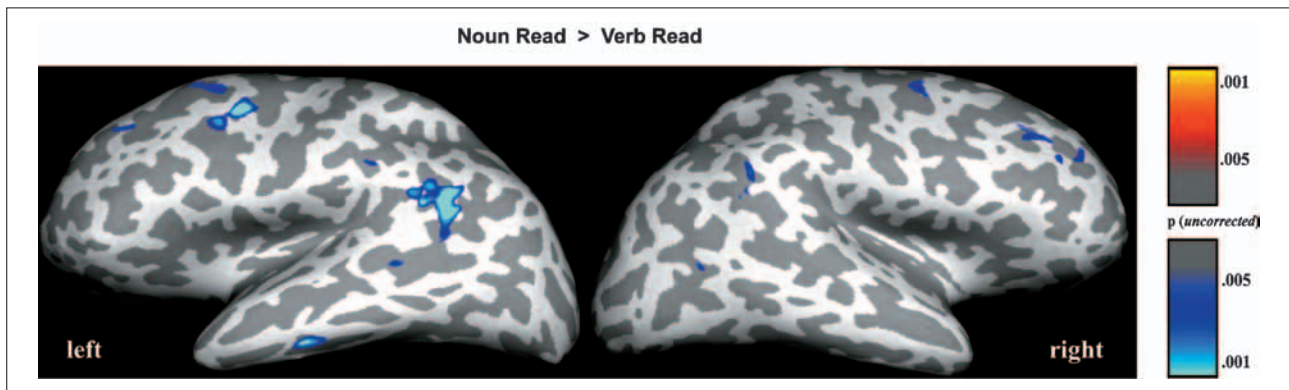
Fig. 5 – *Silent reading of nouns versus verbs (p < .005, uncorrected). Negative activations in this contrast (blue) show regions where reading verbs yields greater activation than reading nouns.*
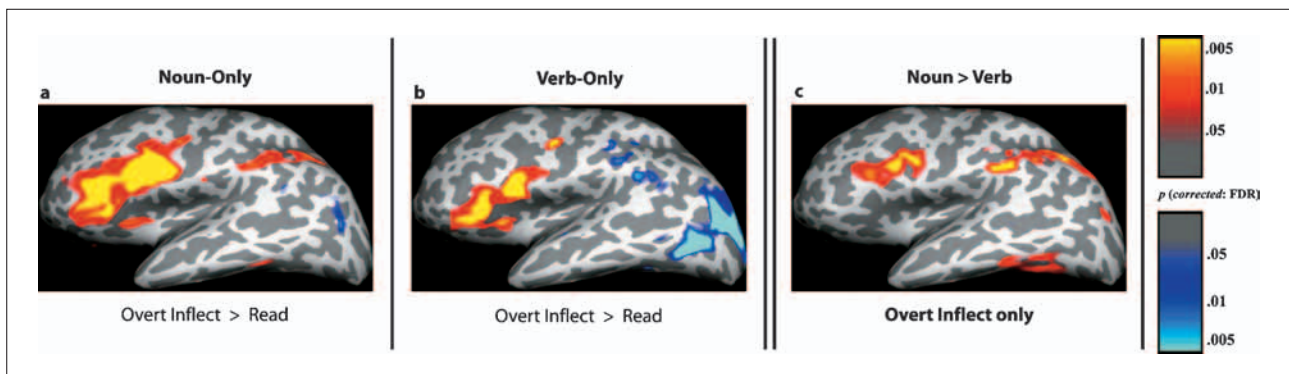

Fig. 6 – *Noun versus verb inflectional processing. Results (p < .05, corrected) of the Overt-Inflect > Read contrast as in Fig. 3b but performed separately for (a) nouns and (b) verbs. (c) Results of a direct contrast between nouns and verbs within only the Overt-Inflect task.*

inhibited when the brain switches to a goal-directed mode of operation. Convergently, the locus of the electroencephalography (EEG) alpha rhythm (stereotypical of calm or resting states) has been traced to similar brain regions (Martinez-Montes et al., 2004; Miwakeichi et al., 2004). It is possible that our Read task is best performed relatively automatically, with the brain closer to its default mode, and that this mode is actively inhibited in the more attention-demanding Inflection tasks.

Common Pathway for Inflection of Nouns and Verbs

As mentioned in the Introduction, evidence from aphasiology, neuroimaging, and psycholinguistics suggests that nouns and verbs may differ in their patterns of cortical representation, though there are disagreements on whether the differences are based on the categories themselves or on their characteristic meanings (Caramazza and Shapiro, 2004; Shapiro et al., 2001; Gentner, 1981; Luzzatti et al., 2002; Perani et al., 1999; Pulvermuller et al., 1999a, 1999b). In the present investigation, the Read task allows an approximate comparison to the tasks used in most of the previous noun-verb studies. The comparison of simple reading of nouns and verbs (Figure 5) yielded results generally convergent with Perani et al. (1999), namely that the only regions showing

significant differences were those with a greater response to verbs; none showed a greater response to nouns. Moreover, the verb-selective regions were in lateral temporal and dorsolateral prefrontal cortices. Compared to Perani et al. (1999), the present frontal activations were more dorsal, in premotor areas, and activations were more bilateral. Since there were so few activated voxels, the FDR method failed to produce a corrected threshold, so an uncorrected threshold of p < .005 was used. This contrast defines a reference point for considering noun-verb differences in inflection.

The overt inflection tasks used in this experiment could exaggerate such differences, as the verb inflection was past tense, which refers to the inherently verb-relevant semantic feature of time, whereas the noun inflection was plural, which refers to the inherently noun-relevant semantic feature of number. If the Read results and previous studies indicate the storage or access of noun and verb lexicons, and the process of grammatical inflection takes place where the words are stored, then the differences should be further accentuated in Inflection. Despite these reasons to find differences, the gross pattern of activation in the Overt-Inflect > Read condition (expected to index inflectional processing) showed substantial similarities (Figure 6a and b). The differences predicted by other studies in the literature are separate or greater activations in the temporal lobe

for nouns and in the IFG for verbs. In fact, both contrasts significantly activate roughly the set of areas seen in the global contrast, namely BA 44/45, BA 47, anterior insula, and (not shown in the figure) SMA. There are indeed magnitude differences in these circuits, with nouns showing a stronger response than verbs in BA 44/45 and BA 47, as confirmed by the direct contrast in Figure 6c. These differences may come from the lower frequencies of the nouns (Chee et al., 2002, 2003), and especially from the inflection of the unusual irregular nouns: when only regular forms are included in the contrast, the differences in the magnitude of the significantly activated areas is reduced. There appear to be no categorical differences in the four major frontal areas recruited by the different grammatical categories, which suggests that there may be a common circuit supporting inflectional morphology across different grammatical categories.

The present results confirm and extend those of Tyler et al. (2004). As described in the Introduction, they had subjects make semantic judgments on triplets of inflected words and found a noun-verb difference in the LIFG, which they interpreted as a correlate of morphological processing. Our results converge with theirs in that in both studies the set of regions activated for nouns overlapped almost entirely with the set of regions activated for verbs. The results converge further in that noun-verb differences consisted of activation magnitude within a subset of these shared regions, specifically in regions not traditionally related to lexical storage (viz., the temporal lobes) but rather in those implicated in grammatical processing. The LIFG region implicated in the Tyler study was similar to the LIFG region in the present Noun-Overt > Verb-Overt contrast (Figure 6c), namely the BA 44/45 and BA 47 clusters, mostly in their dorsal extents. These results are not consistent with a model in which words are inflected in the regions in which they are stored, and are more consistent with a model in which words of all classes are processed in a central circuit.

The present results differ from those of Tyler et al. (2004) and Perani et al. (1999), who found voxels that were more active for verbs but none that were more active for nouns. The present results show the opposite pattern. Tyler et al. (2004) attribute their verb-preferential activations to the fact that verb inflection specifies grammatical roles to a greater extent than does noun inflection. The present results show that the class-preference can also be skewed toward nouns; the asymmetry here is likely caused by properties of the stimuli themselves (e.g., their low frequency and non-native irregular patterns) rather than the classes. The fact that multiple factors can affect the asymmetry in degree of activation, while activation itself in this area is seen across all word types,

again points to these frontal circuits being recruited based on the need for inflectional processing, and independent of word class.

At the same time, the present results show a noun-verb difference outside these frontal regions, in the intraparietal sulcus (IPS), that warrants specific consideration (Figure 6c). Other contrasts in this experiment show that this region is not specifically activated by noun inflection; in fact, it is active when subjects perform any of the tasks, in comparison to the fixation baseline condition. Thus the region is not part of the circuit generally recruited for inflection *per se* (Figure 3a). This suggests that the major function of the IPS here is something common to all tasks such as mediating task-related visual attention (Jovicich et al., 2001). The greater IPS activation for inflecting nouns, then, may simply be a consequence of their lower frequency and the unusualness of some of the irregular plurals. However, the activity difference is strong (Figure 6c) and is part of the noun-only and not verb-only inflection contrast (Figure 6a and not b), so it is also worth entertaining the possibility that the IPS may be activated for an additional role related to inherent differences between noun and verb inflection. The IPS is implicated in several cognitive functions, including number cognition (Dehaene et al., 1996; Chochon et al., 1999), which is consistent with the fact that our noun overt inflection task requires discriminating singular and plural number (verbs also mark number, specifically, the number of the subject, but that feature does not need to be computed in the task subjects executed in this study).

Regular and Irregular Inflection

Regular and irregular inflection, as mentioned, have been shown to be linguistically, psychologically, and neurologically distinct, leading to the expectation that neuroimaging studies might show distinct patterns of activation for them, in particular, increased involvement of left inferior frontal areas for regular inflection and of left temporal and parietal areas for irregular inflection. The current results fit with previous neuroimaging studies in failing to show such an association. Figure 7 reveals that there are indeed differences in the brain areas engaged by inflecting regular and irregular forms. This would seem to speak against single-mechanism models of inflection, whether they invoke rules or associative memory. These differences were partially consistent across nouns and verbs (especially in bilateral anterior insular, ventral IFG, and anterior cingulate regions), but were not in conformity with the expected anterior-posterior difference. The verbs showed, if anything, the opposite association, and both nouns and verbs showed increased engagement of inferior frontal areas by irregular inflection.
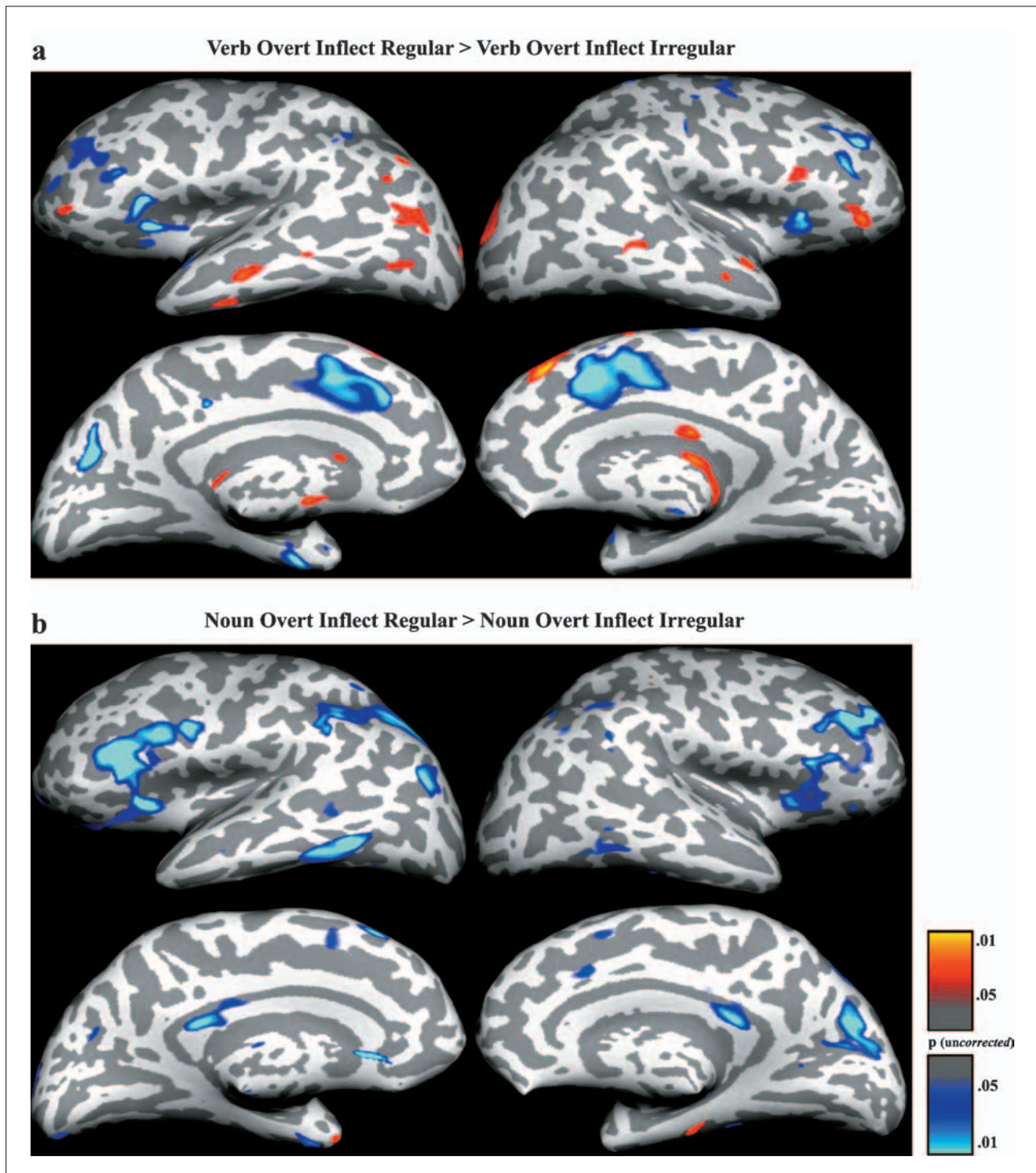
Assuming the observed differences are

a — **Verb Overt Inflect Regular > Verb Overt Inflect Irregular**

b — **Noun Overt Inflect Regular > Noun Overt Inflect Irregular**

Fig. 7 – *Regular and irregular inflection of verbs (a) and nouns (b) in Overt Inflect trials. Since these analyses contrasted data from only one of the twelve conditions, a liberal threshold was used (p < .05, uncorrected).*

systematic, a few tentative interpretations are possible. Especially in the verb results, there was bilateral activation of the medial portion of the SMA and the ACC. These areas have been implicated in the monitoring of conflict and the inhibition of habitual responses, especially in conjunction with lateral frontal regions (Kerns et al., 2004a; Miller and Cohen, 2001; Holroyd et al., 2004). Activation of cognitive control and inhibition regions may be required by irregular inflection for two reasons: blocking of the regular rule to prevent overregularizations (e.g., *bringed*), and suppression of conflicting responses among competing irregular patterns (e.g., *brang* or *brung*) that are generalized from families of similar irregular forms (e.g., *spring – sprang*, *ring – rang*, *drink – drank*, *sing – sang*). The latter explanation would be consistent with the weakness of such activation in the noun data, since irregular nouns do not fall into such phonological families. Jaeger et al. (1996) also showed strong left ACC and middle/posterior cingulate activations preferentially for inflection of irregular past-tense

verbs, with some weaker ACC for the inflection of nonce verbs.

A second systematicity is the involvement of left inferior PFC and bilateral anteroventral prefrontal regions in irregular inflection, paralleling a finding by Rhee (2001) and Rhee et al. (2003), as well as those Broca's aphasics who have difficulty with irregular forms (Penke and Krause, 1999; Penke et al., 1999). These anterior and ventrolateral regions of cortex have been shown to be activated in tasks requiring selection of words from memory on the basis of semantic and lexical cues, such as stem completion (Desmond et al., 1998), generation of a verb related to a target noun (Petersen et al., 1998), and discrimination of abstract from concrete nouns (Demb et al., 1995; Poldrack et al., 1999). The selection of an irregular form from memory based on the intersection of the lexical item and a set of morphosyntactic features, and the suppression of inappropriate words that partly meet such criteria, may engage the same circuit.

Some of the left frontal activations, especially for nouns, are part of the general inflection-related circuits demonstrated in Figure 3. These may be magnitude differences in common neural systems shared by regular and irregular inflection, in addition to or as an alternative to categorical differences in neural systems or processes. For nouns, the irregulars included compounds and Latin/Greek forms, as discussed in the Methods, and the activation difference may index a greater vigilance or attention to inflection of these items.

The medial views in Figure 7a show small regions preferentially activated by regular verb inflection (depicted in red) on the mesial surfaces of the hemispheres, in and below the posterior corpus callosum on the right, and more posterior on the left. These regions do not actually correspond to cortex, because their surface topography in these displays is partly an artifact of the cortical inflation algorithm. Rather, the immediately subjacent regions project through and are visualized on the virtual surface. The regular-specific activations are thus likely to be projections from subcortical structures, though their coordinates and identities are not uniquely identifiable by the methods of reconstruction used in this study. One possibility is that they arise from basal ganglia activity, which would be consistent with the claims of Ullman et al. (1997, 2005) that regular inflection is computed in a circuit that includes the basal ganglia (see also Tsapkini et al., 2001).

A final convergence of the present data with existing studies comes from overall patterns of activity for regulars and irregulars. Many more voxels were preferentially active for irregular inflection than regular inflection, a result found in all previous studies (Jaeger et al., 1996; Sach et al., 2004; Rhee, 2001; Beretta et al., 2003) and reviewed in Beretta et al. (2003).

In the maps for noun inflection, there are regions of preferential activation for irregular inflection in the left inferior temporal cortex, sometimes associated with lexical knowledge of nouns, and left intraparietal sulcus, implicated in visuospatial attention as well as numerical processing (see above). It is possible that these areas are activated by the lexical retrieval of nouns, which is required by irregular but not regular inflection of nouns, nor by either kind of inflection of verbs.

These tentative speculations contrast with the systematicity of the activation maps presented above for inflection in general, and of the patterns of association found in most of the studies of neurological patients. One possibility is that the single-mechanism theory of inflection is correct, and that there are various problems with the patient studies and that the regular-irregular differences in the neuroimaging studies are due to some confounded factor. We suspect that instead the discrepancy arises from the fact that neuroimaging, which reveals the full network of processes implicated in inflection rather than the indispensable ones, is especially sensitive to the ways (discussed in the introduction) in which the regular-irregular distinction maps only imperfectly onto the computation-memory distinction. Future studies may need more subtle manipulations, involving carefully selected subsets of words, rather than an across-the-board regular-irregular dichotomy, to systematically map the effect of irregularity on the interplay between memory and computation.

GENERAL DISCUSSION

Contrasts from fMRI recordings of people engaged in a task that is inherently grammatical yet minimally confounded with semantics, working memory, or articulation rehabilitate the hypothesis that Broca's area and adjacent cortical regions execute abstract grammatical computation. The computation executed there is abstract in the sense that it instantiates inflectional features demanded by the syntax of the sentence rather than the pragmatic demands of the conversational context, and that it embraces both nouns and verbs, both regular and irregular forms, and both unaltered and overtly altered forms.

The current data are consistent with models of language organization in the brain that attribute a role to Broca's area (and associated regions) in grammatical processing (e.g., Newman et al., 2003; Embick et al., 2000). At the same time, they do not show that grammar is the only function computed in Broca's area, that Broca's area is the only region implicated in grammatical processing, or that the language-related function of Broca's area is applicable only to language. What they show is

that Broca's area appears to have a key role in the computation of grammar that cannot be attributed to generic cognitive processes.

The results, moreover, refine the functional mapping of grammatical computation in the left frontal regions of the brain. The anterior insula appears to be more selective to manipulation of overt phonological material, along with the medial SMA and BA 45. Parts of BA 44 and BA 47 are also involved in phonology, while distinct regions of BA 44 (more ventral) and BA 47 (more dorsal) may be tied to the computation of abstract grammatical features *per se*, even when there is no difference in the computation of overt phonology. The findings show that spatial patterns of brain activity can in some ways, but not others, be transparently mapped onto decompositions of cognitive tasks arrived at by analyses of the computational requirements of the tasks. Successes in the present experiment include the fact that overt inflection activated a superset of the areas activated by zero inflection (when both are compared to the Read task), and that regular and irregular inflection elicit partially non-overlapping sets of neural activation, including regions that are plausibly tied to the blocking of the regular rule by irregulars. One of the failures of simple correspondence between task components and brain activation patterns is the fact that reading a word does not activate only a subset of the areas activated by inflection but rather includes areas that might be engaged by strategies specific to the reading-aloud task; this raises a note of caution for studies using simple reading as the only baseline task. Another is the finding that most of the regions that differentiate regular and irregular inflection are not explained by otherwise well-supported generalizations that attribute regular inflection to grammatical computation in frontal regions and irregular inflection to lookup in temporal or parietal regions. This in turn suggests that more attention be given in future studies to the ways in which different regular and irregular forms enlist different combinations of lookup and computation.

Previously, the involvement of Broca's area in language has been attributed both to more general and to more specific factors. The generalized working memory models of Just et al. (1996) would not appear to apply to our results, because the simple morphological task should not require heavy demands on working memory (compared to, say, a reading span task), and also because the different conditions do not vary the number, duration, or complexity of items held in mind. For similar reasons, the specifically parsing-related working memory of Caplan and Waters (1999) also would not seem to apply, because the experimental contrasts (especially Over-Inflect *vs.* Zero-Inflect) do not vary the number of linguistic heads that must be maintained or the duration of the maintenance, nor is there an ambiguity to resolve.

Also unclear is how semantic selection demands, such as those invoked by Thompson-Schill et al. (1997), would map to the current task. If anything, the Zero-Inflect task required more features to be evaluated in order to determine the correct form (third person, plural number, present tense, and imperfective aspect) than did the Overt-Inflect task (past tense). Yet it was the Overt-Inflect task that evoked greater recruitment of inferior frontal regions. Moreover, though both inflection tasks involve morphosyntactic features, and such features do have minimal semantic content, the features do not *have* to have such content, such as in languages with inflections sensitive to grammatical gender or arbitrary declensions and conjugations. Even in English, the semantic selection in inflection is secondary to the demands of grammatical computation (Does the clause have to be tensed? Does the noun appear with an article requiring number concord?) rather than in service of communication in the conversational context. Finally, general articulatory demands (Wise et al., 1999) are ruled out by the Zero-Inflect > Read contrast, in which motor output is identical, while the abstract grammatical features vary.

What about theories attributing *greater* specificity to Broca's and associated areas? The hypothesis advocated by Grodzinsky (1986b, 1989, 2000) that the role of Broca's area is purely the binding of traces and moved elements does not predict the present results, since the task involves only two- or three-word context frames without moved elements (at least in traditional theories of syntactic movement), nor do the contrasts among conditions involve moved elements. It is true that recent theories in the Chomskyan framework do attribute inflection to movement. Roughly, the inflectional morpheme moves from an underlying position as the head of an inflection phrase (such as a Tense Phrase) onto the head of the verb phrase in its complement position, in order to become bound as an enclitic tense-marking affix (see Baker, 2001). If so, the present task would in fact involve movement, consistent with Grodzinsky's (1986b, 2000) hypothesis. Note, however, that in these theories movement and traces are not restricted to the plausible relationships between antecedents and gaps, such as in passive constructions, relative clauses, and *wh*-questions, which have some degree of psycholinguistic support and which were the original motivation for Grodzinsky's (1986b) theory. Rather, movement is so ubiquitous in these theories (largely for reasons of theory-internal consistency) that it is virtually indistinguishable from grammar itself. Also, note that theories of this type typically posit zero-affixes, which occupy determinate positions in grammatical structures and are identical to overt affixes except in lacking a phonological specification. This removes any grammatical difference between the Overt-Inflect and Zero-Inflect conditions, so it is hard to see how the greater

activation elicited by the Overt inflection condition can be explained.

The question of whether Broca's Area involvement in language is domain-general is separate from whether Broca's area itself has domain-general functionality. The first question pertains to whether the processes that activate Broca's during language tasks (or which are destroyed when it is lesioned) are general cognitive abilities like working memory, or are specifically involved in grammatical computation. The current data speak to this question, suggesting that the function is not likely to be any of the domain-general explanations provided so far. The second question is whether the anatomical structures included under the label "Broca's area" function outside of language – a question about the roles of a large anatomical structure, rather than about one of the kinds of computation performed by one of its components. For example, Broca's area recently has been implicated in imitations of human movements (Iacoboni et al., 1999) and in musical syntax (Maess et al., 2001), among other tasks. To interpret these findings, one must keep in mind that "Broca's area", even in the most restrictive definition, is a swath of tissue containing at least 100 million neurons, and it sits on prime real estate in terms of connectivity with known cognitive functional regions of the PFC. While fMRI and lesion studies treat Broca's area as a single module or a few units, it may in fact be composed of numerous functional subunits, which may not necessarily be defined in terms of neatly defined macroscopic anatomical territories.

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