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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