The Role of Broca's Area in Sentence Comprehension

Corianne Rogalsky[1] and Gregory Hickok[2]

Abstract

■ The role of Broca's area in sentence processing has been debated for the last 30 years. A central and still unresolved issue is whether Broca's area plays a specific role in some aspect of syntactic processing (e.g., syntactic movement, hierarchical structure building) or whether it serves a more general function on which sentence processing relies (e.g., working memory). This review examines the functional organization of Broca's area in regard to its contributions to sentence comprehension, verbal working memory, and other multimodal cognitive processes. We suggest that the data are consistent with the view that at least a portion of the contribution of Broca's area to sentence comprehension can be attributed to its role as a phonological short-term memory resource. Furthermore, our review leads us to conclude that there is no compelling evidence that there are sentence-specific processing regions within Broca's area. ■

INTRODUCTION

Broca's area has long been implicated in sentence processing (Goodglass & Kaplan, 1972). Broca's area was first thought to support syntactic processing because Broca's aphasics were found to have agrammatic production (Kean, 1977; Goodglass, 1968, 1976; Gleason, Goodglass, Green, Ackerman, & Hyde, 1975; Goodglass & Berko, 1960). Such patients typically produce syntactically simple sentences that lack function words and inflections (Kean, 1995), suggesting that they are lacking the ability to form syntactic structures. Broca's aphasics also have been found to have difficulty comprehending syntactically demanding utterances such as semantically reversible sentences that contained noncanonical word order ("It was the squirrel that the raccoon chased") (Bradley, Garrett & Zurif, 1980; Caramazza & Zurif, 1976). Such sentences place a heavy burden on syntactic mechanisms because meaning cannot be inferred from lexical–semantic information alone (cf., "It was the nut that the squirrel ate"), nor can typical English-language subject–verb–object word order patterns provide clues to the subject and object of the action (c.f., "It was the raccoon that chased the squirrel"). These deficits in comprehending syntactically complex sentences, along with agrammatic production deficits, suggested an overall syntactic deficit in Broca's aphasia, and thus, linked syntax to Broca's area (Bradley et al., 1980; Caramazza & Zurif, 1976).

Despite early evidence implicating Broca's area in syntactic processing, subsequent studies questioned this view. For example, Broca's aphasics were found to be able to make grammaticality judgments of sentences, even if they are unable to comprehend these same sentences (Wulfeck, 1988; Linebarger, Schwartz, & Saffran, 1983), suggesting that these patients have significant syntactic knowledge available to them (Martin, 2003; Linebarger, 1990; Linebarger et al., 1983). And although some of the earliest functional imaging studies of sentence processing implicated Broca's area, particularly in the comprehension of complex structures (Caplan, Alpert, & Waters, 1998, 1999; Dapretto & Bookheimer, 1999; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996), other studies found a lack of correspondence between sentence processing and activity in Broca's area. For example, Mazoyer et al. (1993) found that activity in Broca's area did not track with the presence or absence of syntactic structure in that it responded not only to meaningful sentences but also to unstructured word lists, and not to structured sentences that were semantically odd. More recently, several studies have found that Broca's area is not activated during the comprehension of spoken normal, meaningful sentences (compared to unintelligible but acoustically similar speech) (Friederici, Kotz, Scott, & Obleser, 2010; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006; Scott, Blank, Rosen, & Wise, 2000).[1] In contrast, another region, the anterior temporal lobe, does appear to track with the presence of syntactic structure in both auditory and visual (written language) modalities, and consequently, this region has emerged as a candidate for supporting syntactic and/or compositional semantic processing (Rogalsky & Hickok, 2009; Humphries, Love, Swinney, & Hickok, 2005; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Vandenberge, Nobre, & Price, 2002; Humphries, Willard, Buchsbaum, & Hickok, 2001; Friederici, Meyer, & von Cramon, 2000; Stowe et al., 1998, 1999). Further, lesion evidence questioned the relation between

[1]University of Southern California, [2]University of California, Irvine

damage to Broca's area and the symptom complex of Broca's aphasia. Specifically, damage to Broca's area alone does not result in Broca's aphasia (Mohr et al. 1978), thus undermining the assumed association between the behavioral deficits and their anatomical source. Thus, the role of Broca's area in sentence processing needs to be re-evaluated.

We will first define Broca's area anatomically and consider what is known about its connectivity patterns. We then consider the empirical evidence behind several hypotheses regarding the role of Broca's area in sentence comprehension.

DEFINITION AND ANATOMY OF BROCA'S AREA

The term "Broca's area" is commonly (and is, for the purposes of this review) defined as the lateral posterior two-thirds of the left inferior frontal gyrus (IFG) (i.e., pars triangularis [PTr] and pars opercularis [PO]) (Figure 1) (Anwander, Tittgemeyer, von Cramon, Friederici, & Knosche, 2007; Aboitiz & Garcia, 1997; Brodmann, 1909). In most brains, the PTr and PO demarcations roughly correspond to Brodmann's areas (BA) 45 and 44, respectively, but the boundaries of BA 44 and BA 45 can vary considerably (Keller, Crow, Foundas, Amunts, & Roberts, 2009; Amunts et al., 1999). Thus, this review will use the gross anatomical terms of PTr and PO because these demarcations correspond more appropriately to the resolution of functional imaging. A third anatomical region, referred to as the frontal operculum (FO) or deep FO, is sometimes noted in discussions of the role of Broca's area in sentence processing (Friederici, Meyer, et al. 2000). In this context, the FO has been described as the inferior–medial portion of the IFG, extending medially to insular cortex and posteriorly to the precentral sulcus (Anwander et al., 2007). The role of this opercular region, although not traditionally designated as a separate part of Broca's area, will also be discussed in this review.

Autopsy-based anatomical studies have identified the arcuate fasciculus as a white matter pathway that connects the posterior superior temporal gyrus (pSTG) with Broca's area (Dejerine, 1895). More recent in vivo tractography studies using diffusion tensor imaging have provided additional details regarding the connectivity of Broca's area. These studies indicated that Broca's area is composed of distinct functional–anatomic subregions. For example, Catani, Jones, and Ffytche (2005) report two distinct pathways connecting Broca's area with temporal regions: a "direct pathway" that links the posterior temporal lobe with Broca's region directly (traditionally labeled as the arcuate fasciculus), and an "indirect pathway" that links the temporal lobe with the inferior parietal lobe and then the inferior parietal lobe with Broca's region (as depicted in Catani et al.'s Figure 3). The indirect pathway projects primarily to PO, whereas the direct pathway projects more anteriorly to include PTr. Glasser and Rilling (2008) also report two frontal–temporal pathways, one connecting the STG with posterior sectors of Broca's area (PO) and another connecting more inferior portions of the temporal lobe, the middle temporal gyrus (MTG), with a more anterior portion of Broca's region that included PTr and surrounding fields. Anwander et al. (2007) report a three-way parcellation separating PO, PTr, and the FO (as depicted in Anwander et al.'s Figure 5). The connectivity of PO with the temporal lobe was primarily via a dorsal route, whereas the connectivity of PTr to the temporal lobe was weighted toward the ventral route. The FO projected to temporal lobe structures via the ventral route. Saur et al. (2008) used functionally defined seeds, one targeting phonological processing and the other targeting higher-level comprehension processes, to define dorsal and ventral pathway projections into Broca's area. The "phonologically" defined seeds were located in the anterior and posterior STG and projected dorsally through the arcuate fasciculus into PO and premotor areas as well as projecting along a ventral route that ran anteriorly in the temporal lobe and through the extreme capsule to the FO.

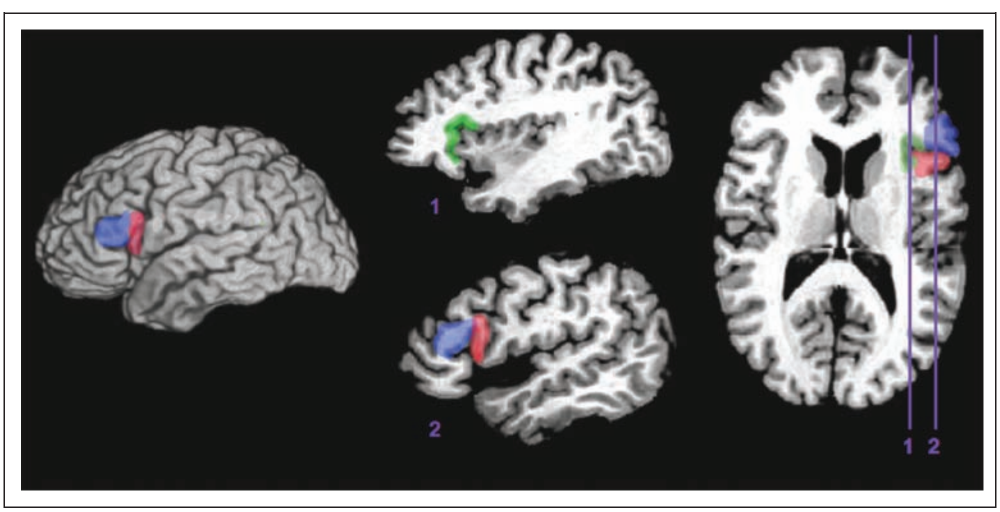

Figure 1. Visualization of Broca's area. Blue = pars triangularis, red = pars opercularis, green = frontal operculum, as defined by Anwander et al. (2007).

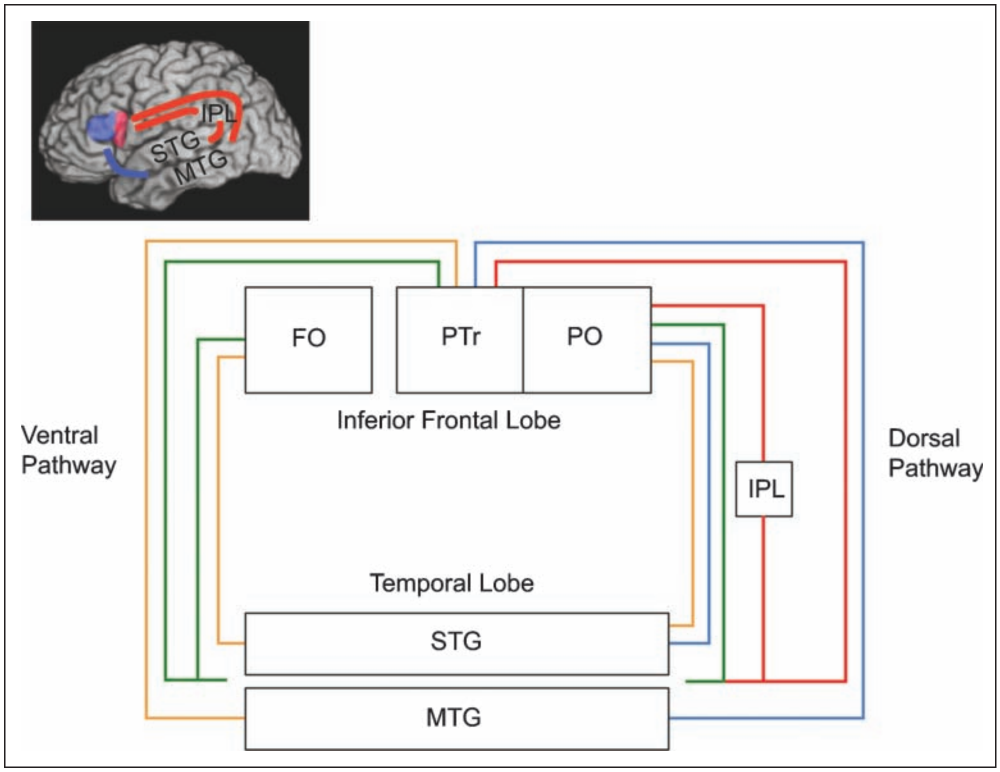

Figure 2. Top left: General map of dorsal (red) and ventral (blue) white matter pathways connecting Broca's area and temporal regions. Bottom center: Schematic diagram of the connectivity of Broca's area with known language-processing temporal regions based on four recent tractography studies. The lines represent the dominant tracts found in each of the studies mentioned above: red = Catani et al.; blue = Glasser & Rilling; green = Anwander et al.; orange = Saur et al. (FO = frontal operculum; PTr = pars triangularis; PO = pars opercularis; STG = superior temporal gyrus; MTG = middle temporal gyrus; IPL = inferior parietal lobule).

The "comprehension"-defined seeds were located in the anterior and posterior MTG and projected only via the ventral route to PTr and the pars orbitalis region anterior to Broca's area. A pictorial summary of these findings is provided in Figure 2, which shows the dominant connections reported in each study.

It is clear from Figure 2 that PO is most densely connected with the STG via the dorsal pathway, PTr is primarily connected with the MTG via both dorsal and ventral pathways, and FO is connected to the temporal lobe primarily via the ventral pathways. Noting the tighter link between PO and dorsal temporal lobe regions that have been implicated in phonological processing, as well as the link between PTr and more ventral temporal lobe regions that have been implicated in semantic processing (Hickok & Poeppel, 2000, 2004, 2007), both Glasser & Rilling and Saur et al. argue that the PO–STG circuit supports phonological-level processes, whereas the PTr–MTG circuit supports higher-order semantic–level processes.

CURRENT HYPOTHESES REGARDING THE ROLE OF BROCA'S AREA IN SENTENCE PROCESSING

There is no shortage of hypotheses regarding the role of Broca's area in sentence processing. We will review six such hypotheses. The first argues for a syntax-specific function, the second for a core property of syntactic processing, but which is not necessarily restricted to syntactic operations, and four more which are more general and are assumed to support syntactic processing indirectly. We will evaluate the evidence both for and against the various hypotheses.

Broca's Area Supports Syntactic Movement

Grodzinsky argues that Broca's area supports a specific aspect of syntactic processing, namely, syntactic movement (Grodzinsky & Santi, 2008; Grodzinsky, 1986, 2000).[2] Syntactic movement refers to elements of the sentence that appear in a position distant from where they are interpreted. For example, in the sentence, *Diogo hates the gift that Jon bought*, the noun *gift* is interpreted as the object of the verb *bought* which appears later in the sentence. This distance between a verb and its object is specific to certain syntactic structures such as relative clauses and does not occur in many other types of structures such as, *Diogo said that Jon bought the gift*. Grodzinsky hypothesizes that Broca's area supports the syntactic computation that processes such displaced elements. Evidence for this anatomical claim has come primarily from two sources. The first comes from the sentence processing ability of patients with Broca's aphasia (and presumed damage to Broca's area),[3] in particular, their difficulty comprehending sentences containing syntactic movement (Grodzinsky, 1989; Schwartz, Saffran, & Marin, 1980; Caramazza & Zurif, 1976). Note that Grodzinsky's anatomical claim is logically independent from his functional claim regarding the nature of the deficit in Broca's aphasia. And although he presents an extensive body of evidence in favor of his functional hypothesis (e.g., Grodzinsky, 2000), the evidence linking the function to the anatomy is thin and relies on an indirect association between Broca's area and Broca's aphasia. As our focus is on the anatomical claim, we will not review the evidence for the functional claim here.

The second source of evidence for the claim that Broca's area supports the processing of syntactic movement comes from functional imaging. Several studies have presented participants with sentences in which the distance is varied between the moved element and its point of interpretation (e.g., *Diogo hates the gift that the girl with the yellow clipboard bought* vs. *Diogo hates the gift that the girl bought*). Activity in Broca's area is greater for long- than short-distance movement dependencies (Rogalsky, Matchin, & Hickok, 2008; Santi & Grodzinsky, 2007a, 2007b; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Cooke et al., 2002). We will refer to this as the movement distance effect.

There are several problems with the syntactic movement hypothesis as the defining role of Broca's area. One, hinted at above, is that the lesion data do not uniquely identify Broca's area as the source of the comprehension deficits found in Broca's aphasia (Hickok, 2000). Lesions restricted to Broca's area do not cause Broca's aphasia (Mohr et al., 1978; Mohr, 1976). Instead, a much larger lesion is required to produce chronic Broca's aphasia (Dronkers & Baldo, 2009; Damasio, 1992). Given that it is chronic Broca's aphasics who exhibit comprehension difficulties on sentences containing syntactic movement, it is impossible to know which part(s) of the lesion are causing the deficit. Furthermore, patients with fluent speech production and lesions that affect posterior brain regions (conduction aphasics) can also exhibit the same sentence comprehension deficits found in Broca's aphasia (Goodglass, Christiansen, & Gallagher, 1993; Caplan, Vanier, & Baker, 1986; Friedrich, Martin, & Kemper, 1985). Thus, an association between syntactic deficits of the sort described by Grodzinsky's theory and damage to Broca's area has not been established.

The functional imaging evidence is also problematic because the movement distance effect is confounded with working memory load. Sentences with longer-distance movement dependencies are harder to process and, therefore, may draw more heavily on domain-general working memory load (Rogalsky et al., 2008; Just et al., 1996; King & Just, 1991). (There have been a handful of attempts to rule out domain-general working memory contributions to the Broca's area activations during sentence comprehension; these will be discussed below in the section on working memory.) In addition, these distance effects may not be observed under all conditions. For example, Caplan, Stanczak, and Waters (2008) found that Broca's area showed a distance effect in semantically unconstrained sentences (e.g., *The lawyer that the banker irritated filed a hefty lawsuit*—a banker can irritate a lawyer and vise versa), but not in semantically constrained sentences (e.g., *The thief that the policeman arrested was known to carry a knife*—policemen can arrest thieves but not vise versa). As both structures are identical in terms of syntactic movement, the syntactic movement theory of Broca's area function predicts a similar pattern of activation independent of semantic content.[4] Another problematic finding in the functional imaging literature is that processing a string of syntactically unstructured words produces as much activation as processing sentences containing long-distance dependencies (Stowe et al. 1998). Nonsentence word lists do not contain syntactic movement and therefore should not result in activation in Broca's area. Word lists have been found to activate Broca's area to equal or greater degrees compared to meaningful sentences in several studies (Humphries et al., 2005; Friederici, Meyer, et al., 2000; Friederici, Opitz, & von Cramon, 2000; Mazoyer et al., 1993), indicating that the Stowe et al. result is not an isolated finding. Findings such as these do not preclude a linguistic-specific role for Broca's area in syntactic movement operations (the region could be multifunctional), but they do raise serious questions about whether a more general process may underlie the region's involvement in sentence processing. The syntactic movement hypothesis, therefore, does not find strong support in the empirical literature.

Broca's Area Supports Hierarchical Processing and the Frontal Operculum Supports Phrase Structure Building

Friederici (2009) has recently argued for two distinct syntactic functions associated with different subregions of Broca's area and vicinity: the FO is argued to support "local phrase structure building" in connection with the anterior temporal lobe, and the PO is argued to support "hierarchical structure processing" in connection with the posterior superior temporal gyrus/superior temporal sulcus (p. 179). It is not entirely clear what the distinction is between these two processes (even local phrase structures are assumed to be hierarchical by most linguistic theories), but presumably, the idea is that the FO is involved in linear concatenation or perhaps less complex hierarchical structures, whereas the PO is involved in processing complex hierarchical structures similar to those required for long-distance movement dependencies. This claim clearly applies to a core aspect of syntactic processing, but according to Friederici, also applies to sequence processing in nonlinguistic domains. The PO–STS/STG circuit is functionally subdivided itself according to Friederici, Makuuchi, and Bahlmann (2009): "Within this network, the left inferior frontal gyrus is responsible for the computation of syntactic structure…. In contrast, the posterior superior temporal gyrus and sulcus … come into play when the interpretation of the thematic relationship of the verb and its arguments is required" (p. 567). Thus, the PO is involved in the more purely structural aspects and the pSTS/STG is involved in the combinatorial semantic aspects. We will focus here on the role of Broca's area and the FO in these proposed functions.

The evidence cited for the FO claim comes from two fMRI studies. One study (Friederici et al., 2003) found that the "left posterior FO" activated more strongly to sentences containing a syntactic violation (e.g., *The blouse was on ironed*) than to sentences that did not contain a violation (e.g., *The shirt was ironed*). This same region was found to be marginally more active for sentences with no-violation compared to baseline, although it did not pass the cluster threshold for significance. The other study examined the brain response to the processing of artificial grammars (Bahlmann, Schubotz, & Friederici, 2008). Subjects were exposed to visually presented consonant–vowel syllable sequences. Syllable sequences were presented according to one of two rules (presented to different groups of subjects). One rule involved only adjacent (linear) dependencies (e.g., [AB][AB]) and one involved hierarchical dependencies (e.g., [A[AB]B]). Once learned, subjects were presented with "grammatical" and "ungrammatical" strings during fMRI scanning. Violations of either grammar type showed activation in the FO, whereas only violations for the hierarchical grammar showed activity in the PO region. This latter finding is evidence for the claim that the PO supports hierarchical structure building.

A subsequent study examined hierarchical processing using natural language stimuli and is offered as further evidence for the PO's involvement in hierarchical structure building (Makuuchi, Bahlmann, Anwander, & Friederici, 2009). This study used a 2 × 2 design with structure (hierarchical vs. linear) and distance (long vs. short) as the factors. Hierarchical stimuli involved written German sentences that were center-embedded (e.g., *Maria who loved Hans who was good looking kissed Johann*), whereas the linear stimuli were non-center-embedded (e.g., *Achim saw the tall man yesterday late at night*). Again, the notion that non-center-embedded sentences are linear is puzzling (see below for a discussion). The number of words between the main subject (noun) of the sentence and the main verb served as the distance manipulation. Restricting their analysis only to the left IFG, Makuuchi et al. report a main effect of structure in the PO, a main effect of distance in the inferior frontal sulcus, and no significant interactions. This finding was interpreted as evidence for distinct localizations supporting hierarchical structure building on the one hand (PO) and nonsyntactic verbal working memory related processes on the other (inferior frontal sulcus), which was operationalized by the distance manipulation.

There are several problems with Friederici's (2009) proposal. First, the PO, which is claimed to support hierarchical structure building, does not activate regularly during the presentation of hierarchically structured stimuli such as natural spoken language sentences. For example, Friederici et al. (2003) report, "For the processing of correct sentences, no reliable activity was observed in classical inferior frontal areas such as BA 44 [~PO]…" (p. 172). This finding is consistent with a number of studies that failed to see activity in Broca's area when contrasting structured sentences with unstructured lists of words or with unintelligible acoustic control stimuli (Rogalsky & Hickok, 2009; Humphries, Binder, Medler, & Liebenthal, 2006; Humphries et al., 2005; Friederici, Meyer, et al., 2000; Friederici, Opitz, et al. 2000; Stowe et al., 1998; Mazoyer et al., 1993).

Second, the study by Makuuchi et al. (2009), which appears to provide the strongest evidence for an association between PO and hierarchical structure processing, is problematic conceptually as well as confounded. Conceptually, the notion of "hierarchical" is defined very idiosyncratically to refer to center-embedding. This contradicts mainstream linguistic analyses of even simple sentences which are assumed to be quite hierarchical. For example, the English translation of a "linear" sentence in Makuuchi et al. would have, *minimally*, a structure something like, *[Achim [saw [the tall man] [yesterday late at night]]]*, where, for example, the noun phrase *the tall man* is embedded in a verb phrase which itself is in the main sentence clause. Most theories would also assume further structure within the noun phrase and so on. Thus, in order to maintain the view that the PO supports hierarchical structure building, one must assume that (i) center-embedded structures involve more hierarchical structure building than non-center-embedded structures, and (ii) that hierarchical structure building is the *only* difference between center-embedded and non-center-embedded structures (otherwise the contrast is confounded). Makuuchi et al. make no independent argument for assumption (i), and assumption (ii) is false in that center-embedded sentences are well known to be more difficult to process than non-center-embedded sentences (Gibson, 1998), thus there is a difficulty confound. One might argue that center-embedded structures are more difficult *because* they are hierarchical in a special way. However, the confound persists in other ways. If one simply counts the number of subject–verb dependencies (the number of nouns that serve as the subject of a verb), the "hierarchical" sentences have more than the "linear" sentences. It is perhaps revealing that the activation response amplitude in the PO to the various conditions qualitatively follows the pattern of the number of subject–verb dependencies in the different conditions: "hierarchical long" (HL) = 3 dependencies, "hierarchical short" (HS) = 2 dependencies, "linear long" (LL) = 1 dependency, "linear short" (LS) = 1 dependency, which corresponds with the pattern of response to these conditions in PO which is HL > HS > LL ≈ LS (see Makuuchi et al.'s Figure 2). Another potential issue involves the use of written stimuli. Although we do not wish to address this issue in detail here, it is worth noting that the studies cited above which did not find evidence for activation of the PO during the processing of structured sentences all used auditory stimuli, whereas the Makuuchi et al. study used visually presented stimuli (and found PO activation even for "linear" stimuli). If Makuuchi et al.'s effects are specific to written presentation, it would indicate a process that is not specifically linked to hierarchical structure building, a function that should operate also in auditory sentence processing.

A second problem for Friederici's proposal concerns the FO, which she argues is involved in local phrase structure building. This hypothesis predicts that the FO should be active during the processing of any sentence. However, in Friederici et al. (2003), the FO was only marginally activated by sentences without syntactic violations, reaching significance only when the sentences contained violations. This is consistent with a previous study (Friederici, Meyer, et al., 2000) that reports "the deep frontal operculum only showed minimal activation for the normal speech condition" (p. 296), which was comparable to activation elicited by word lists, but activated significantly more robustly during the presentation of nonsense sentences (e.g., *The mumphy folofel fonged the apole trecon*). Furthermore, there was a length confound in the Friederici et al. study such that sentences with violations were longer than sentences without violations. It is therefore unclear whether the FO is responding more to the syntactic violations or simply the increase in length. At best, these studies suggest that the FO is responding more to aberrant language processing situations than to local phrase structure building.

Finally, there are inconsistencies across studies regarding both the localization of the FO and its function. For example, one study using artificial grammars reports that the FO is equally sensitive to hierarchical and nonhierarchical grammars (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006); this is Friederici's predicted effect in that both hierarchical and nonhierarchical stimuli should involve local phrase structure building. However, a follow-up study that also used artificial grammars failed to report any effects within the FO, but does report an "anterior insula" site, that is within a centimeter of the FO activation in the first study that responded more to hierarchical than nonhierarchical grammars (Bahlmann et al., 2008). If this anterior insula activation is a different functional region, then this means the original finding of FO activation for artificial grammar processing failed to replicate. If it is the same functional region, then (i) the functional response properties reported in the first study (hierarchical = nonhierarchical) failed to replicate, and (ii) it raises the question of whether the critical structure is the anterior insula rather than the FO. As the anterior insula has been implicated in speech articulation (Dronkers, 1996), one would then question whether the effect has more to do with subvocal articulation than structural processing per se. Another study (Friederici, Meyer, et al., 2000) reports a "deep frontal operculum" site that (i) responds more to "syntactic prose" (nonsense sentences) than normal meaningful sentences, both of which involve structural processing, and (ii) responds with equal amplitude to normal sentences and word lists, where only the former involves structural processing. Finally, yet another study reports an "anterior insula" site that shows sensitivity to *semantic* violations in sentences (Friederici et al., 2003). Table 1 summarizes these observations and serves to highlight the fact that both the location and claimed functional properties of the FO are dubious.

In summary, the claim that the PO and FO are involved in distinct forms of structural processing (hierarchical and local phrase structure, respectively) is not supported by the empirical record, nor is the more general possibility that either of these structures are involved in *any* kind of fundamental syntactic computation as these areas either do not activate during the presentation of natural, syntactically structured stimuli or they are not selective for structured stimuli in that they seem to be activated at least as much, if not more, by unstructured word lists (although the regions could be multifunctional). Furthermore, the idea that portions of Broca's area are critical for functions as basic as hierarchical processing or local phrase structure building suggests that damage to Broca's area should be associated with rather severe global syntactic deficits. Yet, as noted in the Introduction, this is not the case: patients with Broca's aphasia (and therefore large left frontal lesions) have access to much syntactic knowledge (Linebarger et al.,

Table 1. Coordinates and Properties of Peak Activations from Functional Imaging Studies Implicating Regions Labeled as "Frontal Operculum" or "Anterior Insula" in Structural Processing

Study	*Functional Response*	*Reported Location Label*	*Talairach Coordinates*
Friederici et al. (2006)	Equally sensitive to violations of both hierarchical and nonhierarchical grammars	Frontal operculum	−36, 16, 0
Bahlmann et al. (2008)	Hierarchical > nonhierarchical artificial grammar	Anterior insula	−28, 18, 4
Friederici et al. (2003)	Sensitive to semantic violations	Anterior insula	−37, 9, 8
Friederici et al. (2003)	Sensitive to syntactic violations	Posterior frontal operculum	−41, −2, 13
Friederici, Meyer, et al. (2000)	Syntactic prose > normal sentences	Deep frontal operculum	None provided
Friederici, Meyer, et al. (2000)	Normal sentences = word lists	Deep frontal operculum	None provided

1983). In some ways, then, the proposal that Broca's area supports functions such as hierarchical processing and local phrase structure building is a throw back to early, and long since rejected, theories regarding global syntactic processing in Broca's area. As such, these new functional neuroimaging-derived proposals will have to answer to data brought to bear on older theories.

The Pars Opercularis Supports Order-related, Linearization Processes

It has recently been suggested that the PO portion of Broca's area supports order-related or linearization processes (Bornkessel-Schlesewsky, Schlesewsky, & von Cramon, 2009; Grewe et al., 2005, 2006; Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005). The basic observation is that activity in the PO increases as a function of expectancy or preferences in the linear order of arguments in the sentence. It is suggested that this explains the movement distance effect in English because there is a preference for the subject of a verb to appear before the object, which is not the case in many long-distance movement sentences. Evidence for this claim has come from several studies that show activation in the PO to be correlated with order expectancies in the absence of any difference in movement. For example, when the preference for an animate argument to precede an inanimate argument is violated, PO activity increases independent of other structural factors (Grewe et al., 2006). Violation of a referentiality preference (items with a more specific referent, e.g., proper names, are preferred before items with a less specific referent, e.g., plural nouns) has also been shown to modulate PO activity (Bornkessel-Schlesewsky et al., 2009). Thus, the result here is similar to the finding described above that semantically driven expectations can modulate the response to sentences in Broca's area beyond any movement distance effect (Caplan, Chen, & Waters, 2008; Caplan, Stanczak, et al., 2008).

Findings such as these further undermine a syntactic-specific or hierarchical processing basis for Broca's area activation in sentence processing, at least with respect to the PO. However, do these findings suggest a computational operation specifically dedicated to "linearization" or some form of argument order manipulation during comprehension? It is certainly possible, but not necessarily so. As with long-distance dependencies and "hierarchical sentences," there may be a processing load difference associated with violated linear order expectances. That is, it seems possible that when expectancies are violated, processing load may increase, requiring the allocation of additional processing resources, that is, working memory, to the task at hand. This does not mean that some form of working memory is driving the activation in Broca's area, but it is a possibility that must be assessed and ruled out if one wants to claim that the region supports a linguistic-specific process. We address this possibility next.

Broca's Area Supports Working Memory

It is uncontroversial that Broca's area, the PO in particular, is activated in verbal working memory tasks (Buchsbaum & D'Esposito, 2008; Buchsbaum, Olsen, Koch, & Berman, 2005; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Smith & Jonides, 1997; Awh et al., 1996; Smith, Jonides, & Koeppe, 1996) and, accordingly, some authors have suggested that Broca's area supports sentence processing in a nonspecific way via its role in some form of general working memory (Rogalsky et al., 2008; Kaan & Swaab, 2002; Just et al., 1996). Others have argued that Broca's area supports a syntactic-specific form of working memory (Fiebach et al., 2005). There have been a few attempts to address this issue directly.

Santi and Grodzinsky (2007a, 2007b) report on two studies that compared sentences with syntactic movement versus sentences with reflexive binding. Reflexive binding refers to pronoun constructions such as *John knows that Mary pinched herself*, where the pronoun must be interpreted in relation to an element that occurred previously in the sentence. This is nominally similar to the situation in syntactic movement as in, *John loves the woman that David pinched*, where one element (*the woman*) must be interpreted in relation to another distant element (the object of the "pinching"). The authors reasoned that both reflexive binding and syntactic movement involve working memory, and so if Broca's area supports sentence processing only via working memory, both sentence types should activate Broca's area equally. Both studies found that the two types of sentences modulated distinct regions within Broca's area, but the details of which area was modulated by which construction type was contradictory across studies. One study found that syntactic movement was associated with activity in the PO and reflexive binding with activity in the PTr (Santi & Grodzinsky, 2007a), and the other study found the reverse association (Santi & Grodzinsky, 2007b). The discrepancy may have resulted from the different experimental approaches used in the two studies (subtraction versus parametric load modulation). But no matter the explanation, the use of reflexive binding constructions may be a poor tool for assessing the role of nonspecific working memory in sentence processing because these sentences differ in an important respect. In syntactic movement constructions, the existence of a dependency relation is evident early on in processing: Upon hearing the fragment, *John loves the woman that* …, it is already evident that *the woman* needs to be associated with a yet-to-be-encountered element and there is evidence that the syntactic processing mechanism actively searches for this element (Frazier & Flores d'Arcais, 1989; Stowe, 1986; Crain & Fodor, 1985). This is not the case in reflexive binding constructions as there is no cue in the sentence indicating a dependency relation prior to encountering the reflexive pronoun. Clearly then, these two constructions involve different kinds of operations that may differentially tax working memory.

A study by Caplan, Alpert, Waters, and Olivieri (2000) took a more direct approach by assessing the role of a specific type of working memory, phonological short-term memory, in sentence comprehension. Their study compared neural activity during the comprehension of written sentences with shorter- versus longer-distance syntactic movement dependencies during articulatory suppression (repeatedly articulating a word or sequence of syllables). Articulatory suppression interferes with phonological short-term memory by preventing the use of articulatory rehearsal (Baddeley, Thomson, & Buchanan, 1975). In a functional imaging context, one can use articulatory suppression to assess the extent to which sentence processing effects in Broca's area reflect articulatory rehearsal: If the longer-distance movement sentences yield greater activation in Broca's area than the shorter-distance movement sentences even during articulatory suppression, then the residual activation can be attributed to mechanisms other than articulatory rehearsal. Caplan et al. report precisely this pattern. During articulatory suppression, they found an increase in activity in a portion of Broca's area for processing sentences with longer- compared to shorter-distance movement. The activation focus was restricted to the PTr sector of Broca's area, a theoretically relevant fact.

Another recent study (Rogalsky et al., 2008) also employed articulatory suppression but sought to determine not only whether there were movement distance effects in Broca's area that survived articulatory suppression but also whether there were areas within Broca's region that show movement distance effects that disappear during articulatory suppression. In other words, how much of the sentence modulation that is typically found in Broca's area (when articulatory suppression is not employed) can be accounted for in terms of simple articulatory processes underlying phonological working memory? Again, shorter- versus longer-distance syntactic movement dependencies were presented (this time auditorily) both with and without articulatory suppression. Without suppression, longer-distance dependencies produced more activation in several Broca's area regions including the PO and the PTr. However, during articulatory suppression, only the PTr showed a distance effect; no effect was found in the PO (Figure 3), consistent with Caplan et al. (2000), indicating that the PO contributes to sentence comprehension only via its role in the articulatory rehearsal component of phonological working memory. But what about the role of the PTr? Is this region supporting some syntactic-specific function? Another condition in the same experiment suggests it is not. In addition to articulatory suppression, Rogalsky et al. (2008) included a finger tapping condition in which subjects comprehended short- and long-distance dependencies while tapping a repetitive pattern with their fingers (with no verbal articulation). During finger tapping, the PTr sentence effect disappeared, indicating that finger tapping somehow interfered with whatever process resulted in distance effect in the PTr. This suggests that whatever the PTr may be contributing to sentence processing is not syntax- or even language-specific. It is notable that the PO distance effect re-emerged during finger tapping, that is, when articulatory processes were not suppressed, indicating that the effect of articulatory suppression is specific to the vocal tract-related articulation and not a general effect associated with performing *any* secondary task during sentence comprehension.

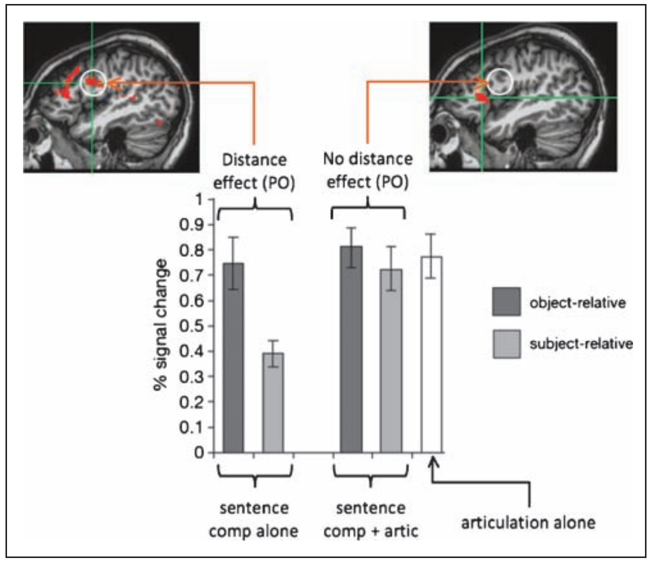

Figure 3. fMRI activation amplitude in the PO and corresponding activation maps during sentence comprehension alone ("sentence comp alone"), sentence comprehension during articulatory suppression ("sentence comp + artic"), and articulation alone. Dark gray bars: long-distance, object-relative sentences; light gray bars: shorter-distance, subject-relative sentences; white bar: articulation alone (no sentence presented). Left activation map shows areas activated more to object- than subject-relative sentences; white circle shows PO region from which bar graphs were generated. Right activation map shows the same contrast under articulatory suppression conditions; note that there is no difference in the PO region (white circle). It is clear that articulatory suppression eliminates the distance effect by saturating the response of the PO region (i.e., the response during subject-relative sentences increases). The fact that articulation alone produces as much activation as comprehending object-relative sentences shows that sentence processing does not account for PO activity once articulation activation is factored out. Figure adapted from Rogalsky et al. (2008).

A more recent attempt to assess the role of verbal working memory and syntactic processing is provided by Makuuchi et al. (2009), as discussed above. As noted earlier, this study manipulated structure (hierarchical vs. linear) and distance (long vs. short). It was assumed that distance manipulation tapped verbal working memory and structure manipulation tapped hierarchical processing. However, as we also noted earlier, the structure manipulation was confounded by difficulty measured either in terms of the number of center-embeddings or in terms of the number of noun–verb dependencies. Thus, the "structure" effect may, in fact, be a working memory effect. A "distance" effect was reported in a distinct region in the inferior frontal sulcus. It was claimed that this effect did not interact with the structure manipulation, however, an examination of the activation graphs for this region show that the "distance" effect was primarily driven by the long hierarchical condition (i.e., the most difficult condition in terms of center-embedding/noun–verb dependencies); this condition had roughly twice the activation level of any of the other conditions, including the long linear condition, which was matched to the long hierarchical condition for distance. It seems that difficulty, and therefore, verbal working memory, may be a major factor in all of the effects reported in Makuuchi et al., despite their claims to the contrary.

To further evaluate the relation between activations produced by articulatory processes and published reports of movement distance effects in Broca's area, we plotted the peak activation foci for movement distance effects from 15 studies on a standard template brain (Figure 4B; because of the confounds in Makuuchi et al. 2009, their data were not included). Group-averaged activation during overt articulatory rehearsal alone from Rogalsky et al. (2008) is also presented for comparison purposes (Figure 4A). Notice that the cluster of movement distance effects around the PO are fully within the region activated during articulatory rehearsal, as is the case with those in the FO. The activation foci in the PTr region, on the other hand, appear to be largely outside the distribution of regions activated by articulatory rehearsal. The blue foci correspond to the two studies that factored out articulatory suppression effects.

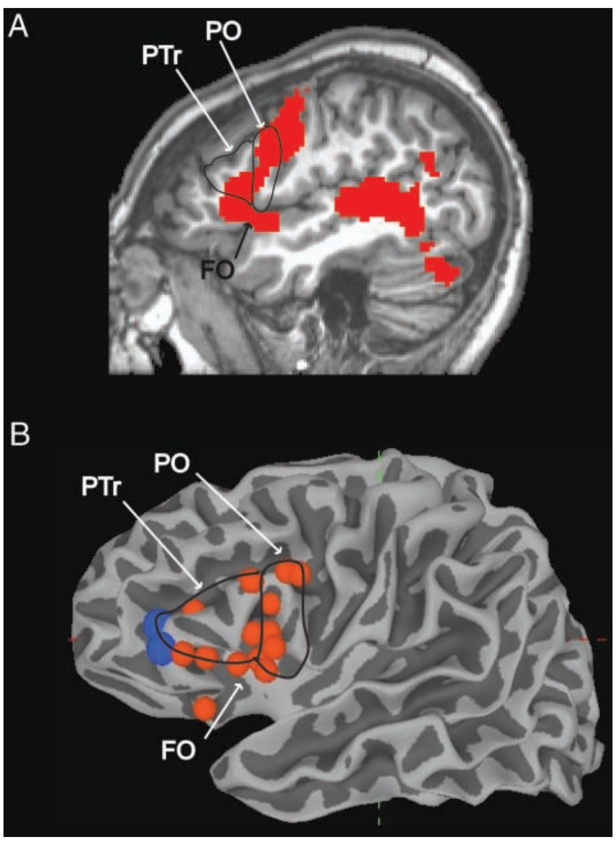

Figure 4. (A) fMRI activation map during overt articulation of meaningless syllables from Rogalsky et al. (2008). Note activation in the PO, in the ventral PTr, and in the FO. (B) Coordinate map meta-analysis indicating peak activations related to syntactic distance effect (orange spheres) and peak activations related to syntactic distance effect during articulatory suppression (blue spheres). Note that most of the syntactic distance effect foci (orange dots) fall within the PO, ventral PTr, and FO, namely, those regions that also activate during simple articulation. Coordinates were mapped onto the cortical surface of an MNI standard brain template using AFNI software's 3dVol2Surf program (see Table 2 for coordinates and citations).

The hypothesis that the PO supports syntactic processing via its role in articulatory rehearsal makes two predictions. One is that preventing articulatory rehearsal in healthy subjects should cause disproportionate decline in the ability to comprehend long-distance dependencies. The other is that damage to the PO should cause articulatory rehearsal deficits. The first prediction holds true. Articulatory suppression results in an increase in errors in comprehending long-distance dependencies but not in comprehending shorter-distance dependencies (Rogalsky et al., 2008). Perhaps what is happening is that for the more difficult long-distance sentences, subjects may use their articulatory rehearsal mechanism to repeat the stimulus back to themselves in order to ensure that their initial interpretation is correct. Articulatory suppression prevents this "second pass," resulting in more errors. Shorter-distance items are less reliant on this second-pass mechanism because they are more often comprehended correctly on the first pass.

The second prediction has not been investigated extensively but a recent study provides partial evidence both for and against this prediction. A group of eight patients with fairly circumscribed lesions involving the IFG were studied on a range of working memory tasks (Baldo & Dronkers, 2006). Predictably, none of them were severely aphasic and none presented with Broca's aphasia as a larger lesion is required to produce that syndrome; four patients only had symptoms of anomia (naming difficulty), three were within normal limits on clinical aphasia testing, and one was "unclassifiable." Results of the working memory tests indicated that patients with IFG lesions did not differ from controls in digit or word span (how many numbers or words can be repeated verbatim) and performed comparable to controls in their ability to repeat entire sentences. This seems to suggest that damage to the PO and vicinity does not cause deficits in phonological working memory. However, these patients were impaired in their ability to make rhyme judgments on pairs of words, particularly when the words were presented visually, and they were impaired on a "two-back" working memory task in which the subject is presented with a sequence of words and must indicate when a given word is the same as that presented two items previously. Both visual rhyming tasks and two-back tasks are argued to rely on articulatory rehearsal, suggesting that the IFG plays some role in this function (Baldo & Dronkers,

Table 2. Talairach Coordinates, Approximate Locations, and Properties of Peak Activations from Functional Imaging Studies Implicating Subregions of Broca's Area in One of the Following: Syntactic Processing, Syntactic Processing during Articulatory Suppression, Semantic Tasks, or Cognitive Control Tasks

Study	*Comparison/Task*	*Coordinates*	*Approx. Location*
Syntax			
Santi and Grodzinsky (2007b)	syntactic movement binding	*−50 31 4*	PTr
Friederici et al. (2006)	parametric modulation of sentence complexity	−49 10 4	PO
Caplan et al. (1999)	syntactic complexity	−52 18 24	PTr
Constable et al. (2004)	syntactic complexity	−49 11 13	PO
Fiebach et al. (2005)	noncanonical word order	−44 21 11, −46 17 4	PTr
		−54 7 28	PO
Moro, Tettamanti, Perani, Donati, Cappa, and Fazio (2001)*	sentence acceptability	−28 34 8	PTr
Friederici, Opitz, et al. (2000)*	function words	−45 12 6	PTr/PO
Dapretto and Bookheimer (1999)*	semantic vs. syntactic judgments	−40 30 14, −52 10 28	PTr, PO
Stromswold et al. (1996)*	syntactic complexity	−46 10 4	PO
Caplan et al. (1998)*	replication of Stromswold	−42 18 24	PTr
Kang, Constable, Gore, and Avrutin (1999)*	syntactic anomaly detection	−50 15 12, −45 25 4	PTr
Caplan, Chen, et al. (2008)	syntactic complexity effect in nonword detection	−44 6 15	PO
Caplan, Chen, et al. (2008)	syntactic complexity effect in plausibility judgment	−49 12 20, −56 10 10	PO
Caplan, Stanczak, et al. (2008)	syntactic complexity with unconstrained thematic roles	*−38 29 −1, −46 23 8*	Porb, PTr
Syntax (during Articulatory Rehearsal)			
Rogalsky et al. (2008)	sentence complexity effect in articulatory rehearsal	−41 33 9	PTr
Caplan et al. (2000)	sentence complexity effect in articulatory rehearsal	−46 36 4	PTr/Porb
Semantic			
Dapretto and Bookheimer (1999)*	semantic vs. syntactic judgments	−46 30 −6	Porb
Wagner, Koustaal, Maril, Schacter, and Buckner (2000)*	priming: semantic judgments	−43 34 12	PTr
Wagner, Pare-Blagoev, Clark, and Poldrack (2001)*	weakly vs. strongly associated words	−45 27 −12, −51 21 −3	Porb
Petersen, Fox, Posner, Mintum, and Raichle (1988)*	word generation	*−33 32 −6, −38 25 8*	Porb, PTr
Buckner, Koustaal, Schacter, and Rosen (2000)*	word stem priming	−43 34 3, −34 31 3	Porb
Thompson-Schill, D'Esposito, Aguirre, and Farah (1997)*	classification: high–low selection	−49 8 30	PTr/PO
Thompson-Schill et al. (1997)*	generation: high–low selection	−38 15 30	PTr

Table 2. (*continued*)

Study	*Comparison/Task*	*Coordinates*	*Approx. Location*
Thompson-Schill, Aguirre, D'Esposito, and Farah (1999)*	generation: new–repeated	−44 15 22	PTr
Muller, Kleinhaus, and Courchesne (2001)*	tone pattern selection	−42 27 −9	Porb
Poldrack et al. (1999)*	semantic vs. case match	−47 20 −3	Porb
Rodd et al. (2005)	high vs. low semantic ambiguity	−42 14 32	PTr/PO
Hagoort et al. (2004)	semantic & world knowledge violations	−44 30 8	PTr
Gold and Buckner (2002)	controlled semantic retrieval	−45 35 −4	Porb
Cognitive Control			
MacDonald, Cohen, Stenger, and Carter (2000)	Stroop task	−41 18 28	PTr
Milham et al. (2001)	Stroop task: incongruent trials	−34 20 24	PTr
Brass and von Cramon (2004)	selection of relevant information	−41 18 26	PTr
Zhang, Feng, Fox, Gao, and Tan (2004)	cued target selection	−42 13 20, −43 24 −1	PTr/PO, Porb
Kouneiher, Charron, and Koechlin (2009)	contextually cued selection	*−45 15 27*	PTr
Nee and Jonides (2009)	perceptual and memorial selection	*−55 14 1, −38 22 14*	PTr
		−36 27 −5	Porb

Asterisks indicate studies summarized in Table 1 of Bookheimer (2002). Italics indicate that the coordinates were originally reported in the study listed in MNI (Montreal Neurological Institute) space, but we have converted the coordinates to Talairach space in this table for consistency. The approximate locations are based on these Talairach coordinates of the peak activations (Porb = pars orbitalis).

2006). We suggest that Broca's area is playing a more complex role in phonological short-term memory than simply articulatory rehearsal because, otherwise, one would expect deficits on simple digit word span tasks. What seems to be affected in patients with IFG lesions is the ability to use articulatory rehearsal to perform a relatively complex task such as rhyme judgment, two-back judgment, or the comprehension of long-distance dependencies. That is, portions of Broca's area may be important for integrating information that is maintained via articulatory rehearsal with higher-order representational systems (phonological, semantic, etc.) and/or decision-level processes. Further research is required to assess this speculation and to determine the focus of these effects with greater anatomical resolution.

To summarize, there is consistent evidence from two studies indicating that what appear to be syntactic effects in functional imaging within the PO can be explained via this region's role in the articulatory rehearsal component of phonological short-term memory. This is consistent with claims coming out of the tractography literature, which ascribe phonological functions to the PO due to its connectivity with the dorsal posterior STG. Only the PTr showed a movement distance effect once phonological short-term memory is factored out of the Broca's activation pattern. This finding is inconsistent with the proposal that PO supports hierarchical structure building via a syntax-specific process. The PTr, on the other hand, is not part of the phonological short-term memory circuit and, consistent with this, receives more of its inputs from higher-order areas in the lateral temporal lobe (e.g., MTG). The PTr then may contribute to sentence comprehension in a way beyond articulatory rehearsal, although it may not be syntax-specific either. Existing lesion evidence suggests a more complex function, however, that requires additional study.

Broca's Area Supports Cognitive Control

It has been suggested that Broca's area supports some aspects of sentence processing via a more general role in "cognitive control," which includes mechanisms involved in resolving conflicts between competing representations or conflicting information (Novick, Trueswell, & Thompson-Schill, 2005). The necessity for conflict resolution arises in a range of language processing situations where ambiguity exists, including phonological, lexical, and sentential contexts. Classic examples of sentence-level ambiguities are found in "garden-path" sentences such as, *Put the apple on the towel into the box*, where an initial analysis (the command to "put the apple on the towel") turns out to be incorrect, requiring a suppression of this initial analysis and the initiation of a revised analysis (do something with the "apple that is on the towel"). Novick et al. propose that Broca's area and surrounding tissue supports the detection of conflicting analyses and the implementation of reanalyses when needed. Support for this hypothesis comes from the observation that classic cognitive control tasks, such as the Stroop task, have been found to activate regions in the vicinity of Broca's area (see Novick et al. for a review), as well as from one study that reported more activity in Broca's region for ambiguous sentences that required reanalysis (Mason, Just, Keller, & Carpenter, 2003) and another (Fiebach, Vos, & Friederici, 2004) that found more activation in BA 44 (~PO) for sentences that were disambiguated later in the sentence compared to earlier in the sentence (late disambiguation is argued to induce more reanalysis load). Although Novick et al. primarily discuss garden-path sentences, one might extend this framework to cases of syntactic movement as these sentences also induce local ambiguities in determining where the displaced item should be interpreted. Additional studies have reported that sentences containing lexically ambiguous words yielded more activation in the PTr than comparable sentences that had fewer word-level ambiguities (Rodd, Davis, & Johnsrude, 2005), and that BA 45 (~PTr) was more active for sentences containing real-world knowledge violations (*Bananas are red and delicious*) compared to those that did not (Hagoort, Hald, Bastiaansen, & Petersson, 2004). Such findings might also be construed as evidence for a cognitive control interpretation of the function of Broca's area because both ambiguities and violations of real-world expectations can lead to conflicts that must be resolved.

An examination of the distribution of activation foci for classic cognitive control tasks shows that they cluster in two distinct regions, one slightly dorsal to the PO and the other in more anterior portions of Broca's area (orange dots in Figure 5). The more anterior cluster is in the vicinity of the movement distance effect foci in the two studies that factored out articulatory processes (blue dots in Figure 5). Interestingly, the same bimodal distribution of activation foci are found in "semantic" tasks, discussed in the next section (green dots in Figure 5). The PO is not typically activated during the performance of classic cognitive control tasks or semantic tasks.

The cognitive control proposal is relatively new and has not been investigated thoroughly across multiple domains and with multiple methods (hemodynamic imaging, lesion). We will therefore have to wait for additional investigation to determine whether it fares any better than the syntax-oriented proposals.

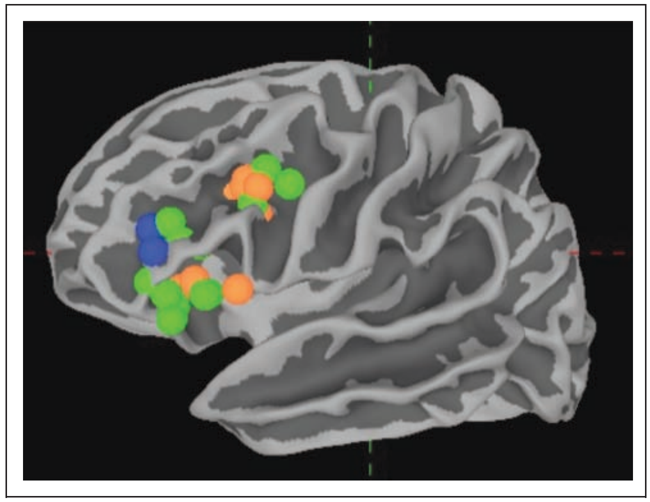

Figure 5. Coordinate map indicating peak activations during cognitive control tasks (yellow–orange spheres), semantic processing (green spheres), and for the syntactic complexity effect during articulatory suppression (blue spheres) overlaid onto the cortical surface of an MNI standard brain template (see Table 2 for coordinates and citations).

Broca's Area is Involved in Semantic Integration

Hagoort (2005) has proposed a framework in which an important function of Broca's region, PTr and BA 47 in particular, is to integrate semantic information into a sentence context.[5] Some of the evidence cited in favor of this view are the semantic effects discussed above (Rodd et al., 2005; Hagoort et al., 2004) as well as a number of older studies that have implicated the IFG in aspects of semantic processing (reviewed in Bookheimer, 2002, and plotted in Figure 5, green dots). This hypothesis is difficult to distinguish from the cognitive control proposal, as anytime there is an increase in the integration demand (e.g., when a sentence violates expectations), one might expect an increased need for conflict resolution and vise versa. As noted, activation distributions for "semantic" and cognitive control effects are largely overlapping. We therefore will not try to distinguish these alternatives here.

Broca's Area Supports Thematic Role Checking/Reanalysis

Caplan, Chen, et al. (2008) and Caplan, Stanczak, et al. (2008) argue that Broca's area is not the primary site of syntactic structure building but instead "supports part of a process of checking thematic roles that are transiently activated during the course of sentence comprehension for their origin in the syntax." The idea here is that for complex sentences with potentially competing thematic role assignments as in semantically unconstrained sentences, a process is initiated to ensure that these thematic roles (who is doing what to whom) are correctly assigned, and this process involves Broca's region. According to Caplan et al., this process may involve reactivating the verbatim form of the sentence via rehearsal and/or a checking process that compares the existing thematic role assignments against the syntax of the sentence to ensure the assignments are correct; if incompatibilities are found, some form of reanalysis would be initiated.

Evidence for this view comes from the finding that a movement distance effect was only found in Broca's area for longer-distance, semantically unconstrained sentences (e.g., where the action was *annoy* and the actors were *banker* and *lawyer*); no distance effect was found in semantically constrained sentences (e.g., when the action was *arrest* and the actors were *policeman* and *thief*) (Caplan, Chen, et al., 2008; Caplan, Stanczak, et al., 2008). As further support for their thematic role checking hypothesis, Caplan et al. cite a previous eye tracking study (Traxler, Morris, & Seely, 2002) which showed more regressive eye movements (re-reading) on exactly these sentence types. Caplan et al. note the similarity between their hypothesis and the cognitive control proposal noted above (Novick et al., 2005) and, in fact, suggest that the processes they propose may be a specific example of a cognitive control process (choosing between competing alternatives). For this reason, we will not try to distinguish these hypotheses here.

SUMMARY

We have considered a range of existing hypotheses regarding the role of Broca's area in sentence processing. The evidence, to date, does not provide strong support for the syntax-oriented proposals. Grodzinsky's syntactic movement hypothesis, which is not specifically tied to any particular sector of Broca's area, is not supported by lesion data in that damage to Broca's area itself has not been specifically linked to sentence comprehension deficits and damage to regions outside of Broca's area can cause the same patterns of comprehension deficit found in Broca's aphasics. The syntactic movement hypothesis also cannot explain why semantically constrained sentences do not show the typical movement distance effects in Broca's area nor why word lists seem to activate Broca's area just as well or better than sentences containing long-distance dependencies. Friederici's proposal also fares poorly in light of the evidence. The PO, which is claimed to support hierarchical structure building, does not activate in all sentence processing conditions that should require hierarchical structure building and fails to show any syntactic effects once phonological short-term memory is factored out of the activation pattern. The FO association with local phrase structure building is also not supported by the evidence as there are questions about its location and whether it responds under conditions which involve the process it is claimed to support. The FO also fails to show any syntactic effects once phonological short-term memory is factored out of sentence processing. Stated more generally, there is no region within Broca's area that shows syntactic-specific effects: The "syntactic" effects found in posterior regions (PO, FO) can be explained in terms of phonological STM and the "syntactic" effects in more anterior regions (PTr) appear to be sensitive to semantic manipulations and/or nonlinguistic tasks such as finger tapping and classic cognitive control tasks. Finally, if Broca's area was supporting processes as fundamental as phrase structure building and hierarchical processing, damage to this region should cause profound syntactic deficits, which appears not to be the case.

Regarding nonspecific accounts, there is mounting evidence that posterior portions of Broca's area (PO) and surrounding regions support sentence comprehension via articulatory rehearsal. It has been shown behaviorally that interruption of articulatory rehearsal disrupts comprehension of sentences, particularly those with long-distance dependencies and that simple articulation activates these posterior portions of Broca's area (Rogalsky et al., 2008). The anatomical connection between PO and superior temporal regions that are involved in phonological-level processes (Hickok & Poeppel, 2007) is also consistent with this conclusion. Additional lesion evidence is required to confirm and clarify these findings.

The function of anterior Broca's area remains unclear. All of the remaining nonspecific proposals discussed in this review implicate some form of integrative or conflict resolution process. The most general of these proposals is Novick et al.'s, which suggests a domain-general cognitive control mechanism. This proposal suffers from the fact that cognitive control as it is studied in nonlinguistic domains activates different regions from those implicated in sentence processing. A more specific model therefore appears necessary. Hagoort's proposal is more specific, implicating semantic integration as a critical function of Broca's area, as is Caplan et al.'s, which further specifies thematic role checking as a central function. The anatomical connection between the PTr and higher-order, possibly semantic-level processes is broadly consistent with these proposals. To our knowledge, there is no evidence that clearly distinguishes between the various proposals of Novick et al. (in a more specific form), Hagoort, and Caplan et al. Perhaps this reflects some degree of convergence. But none of these proposals have been investigated in depth and so should be treated as hypotheses for investigation rather than empirically solid theories.

The question of the role of Broca's area in sentence comprehension is still unresolved and now has moved well beyond language-specific functions and indeed beyond Broca's area itself. We have proposals such as cognitive control and working memory on the table as possible functions and researchers are discussing possible roles of subregions (PO and PTr) as well as regions outside of traditional Broca's area such as the FO, anterior portions of the IFG (pars orbitalis, BA 47), and more dorsal and posterior regions such as premotor cortex (BA 6). These are positive developments. But these developments also complicate the picture. Future studies will have to employ a range of tasks beyond sentence comprehension and a range of manipulations to factor out the possible contributions to activation patterns in the inferior frontal region. More work is also needed regarding the patterns of connectivity in the region, on the functional response properties of connected brain areas, and on the effects of damage or functional disruption to these regions. Such data will further help constrain theory development.

Acknowledgments

We thank Bradley Buchsbaum for sharing his data and generating meta-analysis figures for this article, as well as Jon Sprouse for his input on psycholinguistic issues. This study was supported by NIH grant DC03681.

Reprint requests should be sent to Gregory Hickok, Department of Cognitive Sciences, University of California, Irvine, CA 92697, or via e-mail: greg.hickok@uci.edu.

Notes

1. One study did find greater activation in Broca's area during processing of structured sentences compared to word lists (Snijders et al., 2009), however, this study used visual one-word-at-a-time presentation which may have induced nontypical processing.
2. Grodzinsky and Santi (2008) admit that Broca's area may be multifunctional, possibly with one portion supporting the proposed syntactic functions and other portions supporting functions such as working memory.
3. Although Broca's area is often damaged in Broca's aphasia, damage to this region is neither sufficient (Mohr et al. 1978; Mohr 1976) nor necessary (Dronkers, Shapiro, Redfern, & Knight, 1992) to cause Broca's aphasia. The neural basis of the comprehension pattern often found in Broca's aphasia is less than clear (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004). This complication does not negatively affect the arguments made below, however.
4. An anonymous reviewer suggested that this effect actually implicates a syntactic role for Broca's area because when a sentence is semantically unconstrained, one has to rely on the syntax for comprehension, thus the syntactic processing load is greater for unconstrained sentences. This is certainly a possibility, however, the pattern of results does not support this view in that the presence of semantic constraint led to greater activity to the shorter-distance sentences rather than less activity to the longer-distance sentences. However, as the anonymous reviewer also pointed out, the behavioral effects in this study were atypical, which questions the validity of the hemodynamic findings.
5. Hagoort proposed a broader conceptualization of Broca's area that aligns with other proposals reviewed above, namely, that posterior regions (PO and BA 6) support phonological integration, and PO/PTr support syntactic integration. The phonological claim gains support from the work described above, but the syntactic claim suffers from the same critiques described above: why, for example, do most studies fail to find activation in Broca's area during processing of normally structured sentences?

REFERENCES

Aboitiz, F., & Garcia, G. L. (1997). The evolutionary origin of language areas in the human brain: A neuroanatomical perspective. *Brain Research Reviews, 25,* 381–396.

Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H. B. M., & Zilles, K. (1999). Broca's region revisited: Cytoarchitecture and intersubject variability. *Journal of Comparative Neurology, 412,* 319–341.

Anwander, A., Tittgemeyer, M., von Cramon, D. Y., Friederici, A. D., & Knosche, T. R. (2007). Connectivity-based parcellation of Broca's area. *Cerebral Cortex, 17,* 816–825.

Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in working memory: PET evidence. *Psychological Science, 7,* 25–31.

Baddeley, A. D., Thomson, N., & Buchanan, M. (1975). Word length and the structure of short-term memory. *Journal of Verbal Learning and Verbal Behavior, 14,* 575–589.

Bahlmann, J., Schubotz, R. I., & Friederici, A. D. (2008). Hierarchical artificial grammar processing engages Broca's area. *Neuroimage, 42,* 525–534.

Baldo, J. V., & Dronkers, N. F. (2006). The role of inferior parietal and inferior frontal cortex in working memory. *Neuropsychology, 20,* 529–538.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25,* 151–188.

Bornkessel, I., Zysset, S., Friederici, A. D., von Cramon, D. Y., & Schlesewsky, M. (2005). Who did what to whom? The neural basis of argument hierarchies during language comprehension. *Neuroimage, 26,* 221–233.

Bornkessel-Schlesewsky, I., Schlesewsky, M., & von Cramon, D. Y. (2009). Word order and Broca's region: Evidence for a supra-syntactic perspective. *Brain and Language, 111,* 125–139.

Bradley, D. C., Garrett, M. E., & Zurif, E. B. (1980). Syntactic deficits in Broca's aphasia. In D. Caplan (Ed.), *Biological studies of mental processes*. Cambridge, MA: MIT Press.

Brass, M., & von Cramon, D. Y. (2004). Selection for cognitive control: A functional magnetic resonance imaging study on the selection of task-relevant information. *Journal of Neuroscience, 24,* 8847–8852.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grobhirnrinde in ihren Prinzipien dargestellt aufgrund des Zellenbaues*. Leipzig: Johann Ambrosius Barth Verlag.

Buchsbaum, B. R., & D'Esposito, M. (2008). The search for the phonological store: From loop to convolution. *Journal of Cognitive Neuroscience, 20,* 762–778.

Buchsbaum, B. R., Olsen, R. K., Koch, P., & Berman, K. F. (2005). Human dorsal and ventral auditory streams subserve rehearsal-based and echoic processes during verbal working memory. *Neuron, 48,* 687–697.

Buckner, R. L., Koustaal, W., Schacter, D. L., & Rosen, B. R. (2000). Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain, 123,* 620–640.

Caplan, D., Alpert, N., & Waters, G. (1998). Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *Journal of Cognitive Neuroscience, 10,* 541–552.

Caplan, D., Alpert, N., & Waters, G. (1999). PET studies of syntactic processing with auditory sentence presentation. *Neuroimage, 9,* 343–351.

Caplan, D., Alpert, N., Waters, G., & Olivieri, A. (2000). Activation of Broca's area by syntactic processing under conditions of concurrent articulation. *Human Brain Mapping, 9,* 65–71.

Caplan, D., Chen, E., & Waters, G. (2008). Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex, 44,* 257–275.

Caplan, D., Stanczak, L., & Waters, G. (2008). Syntactic and thematic constraint effects on blood oxygenation level dependent signal correlates of comprehension of relative clauses. *Journal of Cognitive Neuroscience, 20,* 643–656.

Caplan, D., Vanier, M., & Baker, C. (1986). A case study of reproduction conduction aphasia: II. Sentence comprehension. *Cognitive Neuropsychology, 3,* 129–146.

Caramazza, A., & Zurif, E. B. (1976). Dissociation of algorithmic and heuristic processes in sentence comprehension: Evidence from aphasia. *Brain and Language, 3,* 572–582.

Catani, M., Jones, D. K., & Ffytche, D.H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology, 57,* 8–16.

Constable, R. T., Pugh, K. R., Berroya, E., Mencl, W. E., Westerveld, M., Ni, W., et al. (2004). Sentence complexity and input modality effects in sentence comprehension: An fMRI study. *Neuroimage, 22,* 11–21.

Cooke, A., Zurif, E. B., DeVita, C., Alsop, D., Koenig, P., Detre, J., et al. (2002). Neural basis for sentence comprehension: Grammatical and short-term memory components. *Human Brain Mapping, 15,* 80–94.

Crain, S., & Fodor, J. D. (1985). How can grammars help parsers? In D. R. Dowty, L. Karttunen, & A. M. Zwicky (Eds.), *Natural language parsing: Psychological, computational, and theoretical perspectives* (pp. 94–128). Cambridge, UK: Cambridge University Press.

Damasio, A. R. (1992). Aphasia. *New England Journal of Medicine, 326,* 531–539.

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron, 24,* 292–293.

Dejerine, J. (1895). *Anatomie des centres nerveux* (Vol. 1). Paris: Rueff et Cie.

Dronkers, N., & Baldo, J. (2009). Language: Aphasia. In L. R. Squire (Ed.), *Encyclopedia of neuroscience* (Vol. 5, pp. 343–348). Oxford: Academic Press.

Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature, 384,* 159–161.

Dronkers, N. F., Shapiro, J. K., Redfern, B., & Knight, R. T. (1992). The role of Broca's area in Broca's aphasia. *Journal of Clinical and Experimental Neuropsychology, 14,* 52–53.

Dronkers, N. F., Wilkins, D. P., Van Valin, R., Jr., Redfern, B., & Jaeger, J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92,* 145–177.

Fiebach, C. J., Schlesewsky, M., Lohmann, G., von Cramon, D. Y., & Friederici, A. D. (2005). Revisiting the role of Broca's area in sentence processing: Syntactic integration versus syntactic working memory. *Human Brain Mapping, 24,* 79–91.

Fiebach, C. J., Vos, S. H., & Friederici, A. D. (2004). Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers. *Journal of Cognitive Neuroscience, 16,* 1562–1575.

Frazier, L., & Flores d'Arcais, G. (1989). Filler driven parsing: A study of gap filling in Dutch. *Journal of Memory and Language, 28,* 331–344.

Friederici, A. D. (2009). Pathways to language: Fiber tracts in the human brain. *Trends in Cognitive Sciences, 13,* 175–181.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences, U.S.A., 103,* 2458–2463.

Friederici, A. D., Kotz, S. A., Scott, S. K., & Obleser, J. (2010). Disentangling syntax and intelligibility in auditory language comprehension. *Human Brain Mapping, 31*, 448–457.

Friederici, A. D., Makuuchi, M., & Bahlmann, J. (2009). The role of the posterior superior temporal cortex in sentence comprehension. *NeuroReport, 20,* 563–568.

Friederici, A. D., Meyer, M., & von Cramon, D. Y. (2000). Auditory language comprehension: An event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language, 74,* 289–300.

Friederici, A. D., Opitz, B., & von Cramon, D. Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fMRI investigation of different word types. *Cerebral Cortex, 10,* 698–705.

Friederici, A. D., Ruschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex, 13,* 170–177.

Friedrich, F. J., Martin, R., & Kemper, S. J. (1985). Consequences of a phonological coding deficit on sentence processing. *Cognitive Neuropsychology, 2,* 385–412.

Gibson, E. (1998). Linguistic complexity: Locality of syntactic dependencies. *Cognition, 68,* 1–76.

Glasser, M. F., & Rilling, J. K. (2008). DTI tractography of the human brain's language pathways. *Cerebral Cortex, 18*, 2471–3482.

Gleason, J. B., Goodglass, H., Green, E., Ackerman, N., & Hyde, M. (1975). The retrieval of syntax in Broca's aphasia. *Brain and Language, 2,* 451–471.

Gold, B. T., & Buckner, R. L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron, 35,* 803–812.

Goodglass, H. (1968). Studies in the grammar of aphasics. In S. Rosenberg & J. Koplin (Eds.), *Developments in applied psycholinguistic research*. New York: MacMillan.

Goodglass, H. (1976). Agrammatism. In H. Whitaker & H. A. Whitaker (Eds.), *Studies in neurolinguistics* (Vol. 1). New York: Academic Press.

Goodglass, H., & Berko, J. (1960). Agrammatism and inflectional morphology in English. *Journal of Speech and Hearing Research, 3,* 257–267.

Goodglass, H., Christiansen, J. A., & Gallagher, R. (1993). Comparison of morphology and syntax in free narrative and structured tests: Fluent vs. nonfluent aphasics. *Cortex, 29,* 377–407.

Goodglass, H., & Kaplan, E. (1972). *Assessment of aphasia and related disorders*. Philadelphia: Lea and Febinger.

Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2005). The emergence of the unmarked: A new perspective on the language-specific function of Broca's area. *Human Brain Mapping, 26,* 178–190.

Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2006). Linguistic prominence and Broca's area: The influence of animacy as a linearization principle. *Neuroimage, 32,* 1395–1402.

Grodzinsky, Y. (1986). Language deficits and the theory of syntax. *Brain and Language, 27,* 135–159.

Grodzinsky, Y. (1989). Agrammatic comprehension of relative clauses. *Brain and Language, 31,* 480–499.

Grodzinsky, Y. (2000). The neurology of syntax: Language use without Broca's area. *Behavioral and Brain Sciences, 23,* 1–21.

Grodzinsky, Y., & Santi, A. (2008). The battle for Broca's region. *Trends in Cognitive Sciences, 12,* 474–480.

Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences, 9,* 416–423.

Hagoort, P., Hald, L., Bastiaansen, M., & Petersson, K. M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science, 304,* 438–441.

Hickok, G. (2000). The left frontal convolution plays no special role in syntactic processing. *Behavioral and Brain Sciences, 23,* 35–36.

Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory–motor interaction revealed by fMRI: Speech, music, and working memory in area Spt. *Journal of Cognitive Neuroscience, 15,* 673–682.

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4,* 131–138.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition, 92,* 67–99.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8,* 393–402.

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *Journal of Cognitive Neuroscience, 18,* 665–679.

Humphries, C., Love, T., Swinney, D., & Hickok, G. (2005). Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Human Brain Mapping, 26,* 128–138.

Humphries, C., Willard, K., Buchsbaum, B., & Hickok, G. (2001). Role of anterior temporal cortex in auditory sentence comprehension: An fMRI study. *NeuroReport, 12,* 1749–1752.

Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science, 274,* 114–116.

Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences, 6,* 350–356.

Kang, A., Constable, R., Gore, J., & Avrutin, S. (1999). An event-related fMRI study of implicit phrase level syntactic and semantic processing. *Neuroimage, 10,* 555–561.

Kean, M. L. (1977). The linguistic interpretation of aphasic syndromes: Agrammatism in Broca's aphasia, an example. *Cognition, 5,* 9–45.

Kean, M. L. (1995). The elusive character of agrammatism. *Brain and Language, 50,* 369–384.

Keller, S. S., Crow, T., Foundas, A., Amunts, K., & Roberts, N. (2009). Broca's area: Nomenclature, anatomy, typology and asymmetry. *Brain and Language, 109,* 29–48.

King, J., & Just, M. (1991). Individual differences in syntactic processing: The role of working memory. *Journal of Memory and Language, 30,* 580–602.

Kouneiher, F., Charron, S., & Koechlin, E. (2009). Motivation and cognitive control in the human prefrontal cortex. *Nature Neuroscience, 12,* 939–945.

Linebarger, M. C. (1990). Neuropsychology of sentence parsing. In A. Caramazza (Ed.), *Cognitive neuropsychology and neurolinguistics: Advances in models of cognitive function and impairment* (pp. 55–122). Hillsdale, NJ: Erlbaum.

Linebarger, M. C., Schwartz, M., & Saffran, E. (1983). Sensitivity to grammatical structure in so-called agrammatic aphasics. *Cognition, 13,* 361–393.

MacDonald, A. W., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulated cortex in cognitive control. *Science, 288,* 1835–1838.

Makuuchi, M., Bahlmann, J., Anwander, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences, U.S.A., 106,* 8362–8367.

Martin, R. C. (2003). Language processing: Functional organization and neuroanatomical basis. *Annual Review of Psychology, 54,* 55–89.

Mason, R. A., Just, M. A., Keller, T. A., & Carpenter, P. A. (2003). Ambiguity in the brain: What brain imaging reveals about the processing of syntactically ambiguous sentences. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29,* 1319–1338.

Mazoyer, B. M., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., et al. (1993). The cortical representation of speech. *Journal of Cognitive Neuroscience, 5,* 467–479.

Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., et al. (2001). The relative involvement of anterior cingulated and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research, 12,* 467–473.

Mohr, J. P. (1976). Broca's area and Broca's aphasia. In H. Whitaker & H. A. Whitaker (Eds.), *Studies in neurolinguistics* (Vol. 1, pp. 201–235). New York: Academic Press.

Mohr, J. P., Pessin, M. S., Finkelstein, S., Funkenstein, H. H., Duncan, G. W., & Davis, K. R. (1978). Broca's aphasia: Pathologic and clinical. *Neurology, 28,* 311–324.

Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F., & Fazio, F. (2001). Syntax and the brain: Disentangling grammar by selective anomalies. *Neuroimage, 13,* 110–118.

Muller, R., Kleinhaus, N., & Courchesne, E. (2001). Broca's area and the distribution of frequency transitions: An fMRI study. *Brain and Language, 76,* 70–76.

Nee, D. E., & Jonides, J. (2009). Common and distinct neural correlates of perceptual and memorial selection. *Neuroimage, 45,* 963–975.

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective & Behavioral Neuroscience, 5,* 263–281.

Petersen, S. E., Fox, P. T., Posner, M. I., Mintum, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature, 331,* 585–589.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage, 10,* 15–35.

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex, 15,* 1261–1269.

Rogalsky, C., & Hickok, G. (2009). Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex. *Cerebral Cortex, 19,* 786–796.

Rogalsky, C., Matchin, W., & Hickok, G. (2008). Broca's area, sentence comprehension, and working memory: An fMRI study. *Frontiers in Human Neuroscience, 2,* 14.

Santi, A., & Grodzinsky, Y. (2007a). Taxing working memory with syntax: Bihemispheric modulations. *Human Brain Mapping, 28,* 1089–1097.

Santi, A., & Grodzinsky, Y. (2007b). Working memory and syntax interact in Broca's area. *Neuroimage, 37,* 8–17.

Saur, D., Kreher, B. W., Schnell, S., Kummer, D., Kellmeyer, P., Vry, M. S., et al. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences, U.S.A., 105,* 18035–18040.

Schwartz, M. F., Saffran, E. M., & Marin, O. S. (1980). The word order problem in agrammatism: I. Comprehension. *Brain and Language, 10,* 249–262.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. S. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123,* 2400–2406.

Smith, E. E., & Jonides, J. (1997). Working memory: A view from neuroimaging. *Cognitive Psychology, 33,* 5–42.

Smith, E. E., Jonides, J., & Koeppe, R. A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex, 6,* 11–20.

Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J., Petersson, K. M., & Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: An fMRI study using word-category ambiguity. *Cerebral Cortex, 19,* 1493–1503.

Spitsyna, G., Warren, J. E., Scott, S. K., Turkheimer, F. E., & Wise, R. J. (2006). Converging language streams in the human temporal lobe. *Journal of Neuroscience, 26,* 7328–7336.

Stowe, L. (1986). Parsing wh-constructions: Evidence for online gap location. *Language and Cognitive Processes, 1,* 227–245.

Stowe, L. A., Broere, C. A., Paans, A. M., Wijers, A. A., Mulder, G., Vaalburg, W., et al. (1998). Localizing components of a complex task: Sentence processing and working memory. *NeuroReport, 9,* 2995–2999.

Stowe, L. A., Paans, A. M., Wijers, A. A., Zwarts, F., Mulder, G., & Vaalburg, W. (1999). Sentence comprehension and word repetition: A positron emission tomography investigation. *Psychophysiology, 36,* 786–801.

Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain and Language, 52,* 452–473.

Thompson-Schill, S., Aguirre, G., D'Esposito, M., & Farah, M. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia, 37,* 671–676.

Thompson-Schill, S., D'Esposito, M., Aguirre, J. K., & Farah, M. J. (1997). Role of the left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences, U.S.A., 94,* 14792–14797.

Traxler, M., Morris, R., & Seely, R. (2002). Processing subject and object relative clauses: Evidence from eye movements. *Journal of Memory and Language, 47,* 69–90.

Vandenberge, R., Nobre, A. C., & Price, C. J. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience, 14,* 550–560.

Wagner, A., Koustaal, W., Maril, A., Schacter, D., & Buckner, R. (2000). Task-specific repetition priming in left inferior prefrontal cortex. *Cerebral Cortex, 10,* 1176–1184.

Wagner, A. D., Pare-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron, 31,* 329–338.

Wulfeck, B. (1988). Grammaticality judgments and sentence comprehension in agrammatic aphasia. *Journal of Speech and Hearing Research, 31,* 72–81.

Zhang, J. X., Feng, C., Fox, P. T., Gao, J., & Tan, L. H. (2004). Is left inferior frontal gyrus a general mechanism for selection? *Neuroimage, 23,* 596–603.