11 Dissecting the language organ: A new look at the role of Broca's area in language processing

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Early in the nineteenth century, the notion that a mental faculty could be localized to a particular region of the brain was associated with the palpation of the scalps of Victorian men and women in their parlors – hardly the basis for serious scientific pursuits. Reports of selective language impairments following frontal lobe damage (consistent with the phrenologists' localization of language) were largely ignored. But resistance to localism in the scientific community was waning in 1861, when Paul Broca first described the case of Leborgne, rendered speechless (except for the recurrent use of the syllable "tan") by a condition that Broca subsequently attributed to progressive softening of "the middle part of the frontal lobe of the left hemisphere" (1861a, p. 237). Following Broca's reports, and for much of the twentieth century, lesions to the left frontal operculum were linked to a constellation of linguistic deficits affecting the production of words and sentences and the comprehension of certain syntactic structures (i.e., Broca's aphasia). In his argument for a functionally distinct system for articulated language, Broca also laid the foundations for modern cognitive neuropsychology, when he proposed that the independence of a cognitive faculty can be investigated by the careful functional analysis of impaired and spared deficits and by the precise description, "by name and by row [of] the affected convolutions and the degree of alteration of each" (p. 340). Thus, we see in 1861 both a delineation of the general approach of lesion-deficit analyses of the

functional independence of cognitive processes and the specific description of the seat of a "language organ".

THE FACULTY SEARCH: CANDIDATE FUNCTIONS OF BROCA'S AREA

Although the general impact of Broca's work on the field of neuropsychology is immeasurable, the specific question of the function of Broca's area has been reopened in recent years. Systematic investigations of the neural correlates of language disorders generally have found only weak support for historical associations between lesion location and aphasia syndromes; in particular, these methods have revealed that infarction of Broca's area is neither necessary nor sufficient for the syndrome of Broca's aphasia (e.g., Mohr et al., 1978). In contrast to failed attempts to localize aphasia syndromes, lesion analysis of specific deficits has proven to be a more promising way to study the relationship between brain structure and function. Accordingly, recent hypothesized functions of Broca's area have tended to be more narrowly defined than is the syndrome of Broca's aphasia. In this chapter, I briefly review some current hypotheses about the role of Broca's area in articulation, syntax, selection, and verbal working memory. While it is easy to view these as mutually exclusive, this need not be the case; throughout the chapter, I will highlight points of theoretical contact between these hypotheses. In addition, there may not be a *single* function of Broca's area, if simply for the fact that Broca's "area" is not an anatomical area *per se*: the frontal operculum includes at least two cytoarchitecturally distinct regions (Brodmann's areas 44 and 45) and perhaps even more subregions (Amunts et al., 1999; see also Hagoort, this volume). However, for the purposes of simplicity here, I will refer to these regions collectively as Broca's area as I review candidate functions of the frontal operculum in language. Finally, I will consider linguistic impairments that would result from the loss of one putative function: the ability to guide selection among competing sources of information.

The Articulation Organ?

Broca described Leborgne's impairment as a loss of speech (i.e., aphemia), following damage to the organ controlling "the faculty of articulated language, which must not be confused with the general faculty of language" (1861b, p. 331). It was subsequent investigators who saddled Broca's area with the burden of a host of other linguistic functions and dubbed the disorder a loss of language, or aphasia. While it appears that this expansion

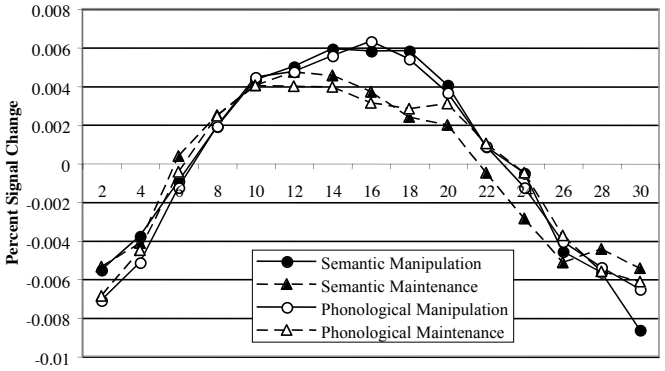

FIG 1. Delay-period activity in Broca's area during maintenance (triangles) or manipulation (circles) of either semantic (filled) or phonological (unfilled) information. Results indicate that the fMRI response in Broca's area is affected by processing demands but not the type of information that is being processed (adapted from Barde & Thompson-Schill, 2002).

of the functions of Broca's area may have been overexuberant, what about Broca's original claim? Is there an independent "faculty of articulated language", and if so, is it controlled by Broca's area?

Some recent neuroimaging studies have supported a role of the left frontal operculum in aspects of speech production (e.g., Indefrey et al., 2001) or phonological processing (Poldrack et al., 1999). Laura Barde and I recently argued against the hypothesis that Broca's area is specialized for phonological processing based on the results of an fMRI study that compared the maintenance and manipulation of semantic and phonological information in a delayed recognition working memory paradigm (Barde & Thompson-Schill, 2002). As shown in Figure 1, we observed modulation of activity in Broca's area as a function of processing demands (i.e., more activity when subjects had to manipulate information during the memory delay than when they passively maintained that information), but no differences between semantic and phonological processing conditions (cf. Gold & Buckner, 2002). Thus, neuroimaging studies are mixed in their support of the claim that Broca's area has a specialized role in speech production or phonology.

Neuropsychological investigations have also failed to support a link between Broca's area and articulatory processes. In a group of patients categorized as Broca's aphasics, impairments in articulation and prosody and the presence of phonemic errors were associated with lesions outside of

Broca's area; patients with lesions restricted to Broca's area displayed normal articulation (Alexander, Naeser, & Palumbo, 1990). Dronkers and colleagues (1996) reported a striking correlation between lesion location and apraxia of speech, an articulatory deficit commonly associated with Broca's aphasia. However, the lesion location they identified was *not* Broca's area. Rather, it was a discrete region of the left precentral gyrus of the insula. It was recently confirmed that Leborgne, too, had extensive subcortical damage including the insula (Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2000). A number of neuroimaging studies also support the role of the anterior insula in overt articulation (e.g., Wise, Greene, Buchel, & Scott, 1999). These findings indicate that Broca may have been correct about the notion of an independent faculty for articulation, although it appears that his localization of that faculty to the left frontal operculum was in error.

The Syntax Organ?

The dominant theoretical and clinical analyses of aphasia in the twentieth century were focused on deficits in language activities (i.e., production and comprehension). The shift away from this description might be credited to the discovery that patients with Broca's aphasia could neither produce *nor comprehend* grammatically complex utterances (Caramazza & Zurif, 1976). Although a group of investigators in the late nineteenth century (including Arnold Pick and Henry Head) had discussed notions of syntax and grammar with regard to aphasia, the most powerful impetus for a reformulation of language deficits came from work in linguistics and psycholinguistics beginning in the 1950's. For example, Chomsky (1981) not only asserted that there was a "language organ" in the mind, but he went on to characterize specific operations, such as those described in his government-binding theory, that were integral to this organ. The loss of these operations is, to some investigators, the defining characteristic of Broca's aphasia (e.g., Grodzinsky, 2000).

As a result of this redefinition of Broca's aphasia, Broca's area now has been hypothesized to be the seat of syntax or, in more recent characterizations, of a specific syntactic operation. Grodzinsky and colleagues have argued that Broca's area "is now thought to house mechanisms that compute dependencies among nonadjacent sentential constituents, established by transformational relations" (2000, p. 83), based not only on their analysis of the syntactic deficits in patients with Broca's aphasia, but also on converging evidence from neuroimaging studies. However, recent reviews of the relevant neuroimaging literature (Friederici, 2002; Kaan & Swaab, 2002) revealed that this structure-function relation is neither specific to Broca's area (i.e., similar patterns of activation are seen

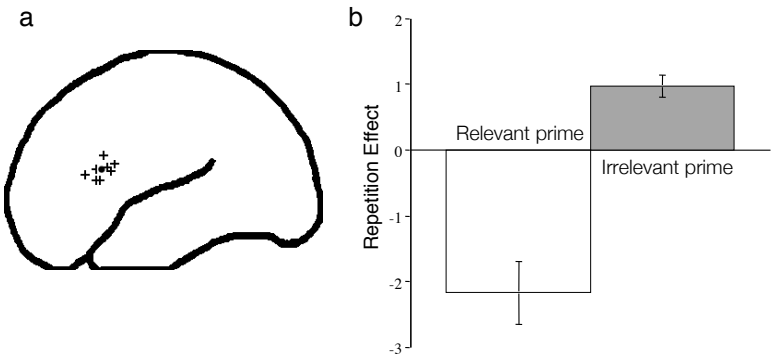

FIG. 2. (a) Foci of fMRI activation in Broca's area in eight subjects during retrieval of color words or action words associated with a target noun (in comparison to word reading); the filled circle indicates the centroid of activation across subjects. (b) The effect of item repetition on activity in Broca's area during word retrieval, when the prime was relevant (unfilled) or irrelevant (filled) information about the item. Priming irrelevant information increased activation in Broca's area (but not in other cortical regions) during word retrieval. Adapted from Thompson-Schill et al., 1999.

throughout frontal and temporal cortices of both hemispheres) nor to syntactic processing (i.e., activation is also observed during non-syntactic, and even non-linguistic, processing). Furthermore, some of the neuropsychological evidence for this hypothesis has been questioned on the grounds that agrammatic sentence comprehension can result from limitations to general processing capacities (e.g., Dick et al., 2001).

The Selection Organ?

In any step along an information-processing stream, an appropriate representation must be selected for further processing. In some cases, selection of a representation may proceed successfully based entirely on local constraints (e.g., bottom-up inputs to a system). However, in other cases, conflict among competing representations may require top-down modulation of the selection process. For example, consider the task of retrieving an action word associated with a given stimulus. In response to the target "scissors", the strongly-associated action "cut" might be activated from the input. In contrast, in response to the target "cat", the activation of many weakly associated actions (e.g., "scratch", "purr") and/or of a strongly

associated non-action (e.g., dog) might fail to produce sufficient activation to select any action representation. Both of these situations (underdetermined representations and prepotent representations) can induce conflict among active representations in working memory that requires top-down intervention (Botvinick, Braver, Barch, Carter, & Cohen, 2001). We suggest that this intervention comes in the form of a modulatory signal from prefrontal cortex that aids in the selection of an appropriate representation (cf. Fletcher, 2000; Miller & Cohen, 2001). This domain-general mechanism is necessary for the successful performance of many tasks, including the ability to identify typeface color instead of reading a word (i.e., the Stroop task; Perret, 1974), to reduce interference during working memory (Thompson-Schill et al., 2002), to maintain fixation instead of making a saccade to a target (i.e., the anti-saccade task; Guitton, Buchtel, & Douglas, 1985), and, as I argue below, for many language tasks as well. That is not to say that the function of Broca's area is domain-general. Rather, we propose that the *mechanism* which enables an organism to select between competing sources of information is a general mechanism implemented by prefrontal cortex that is recruited in different functional domains, both linguistic and non-linguistic; but that may have been harnessed by linguistic systems, perhaps subject to modifications, and perhaps, in this domain-specific form, linked to Broca's area specifically. That is, the ability to select between competing representations may be an example of what Hauser, Chomsky, and Fitch recently dubbed the "faculty of language – broad sense" – a mechanism that is shared with nonhuman animals, that interacts with a more narrowly-defined language system, and that, as such, is responsible for "many of the details of language that are the traditional focus of linguistic study" (2002, p. 1574). Thus, an impairment in this function, which is necessary for some (but not all) linguistic tasks, could be the source of some of the specific symptoms commonly associated with Broca's aphasia.

For nearly a decade, my colleagues and I have been investigating this mechanism and its link to Broca's area. Initially, we observed that the systematic manipulation of selection demands during semantic processing effectively modulated the fMRI response in Broca's area (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Subsequent studies have shown that this effect is not found in other cortical areas involved in language, such as temporal cortex (Thompson-Schill, D'Esposito, & Kan, 1999), is not limited to production tasks or to certain stimulus types, such as verbs (Thompson-Schill et al., 1997) , is not an effect of response conflict (Barch, Braver, Sabb, & Noll, 2000), and is not simply a reflection of task difficulty (Thompson-Schill et al., 1999). Rather, it appears that activity in Broca's area is modulated by increasing demands to select a representation among competing sources of information.

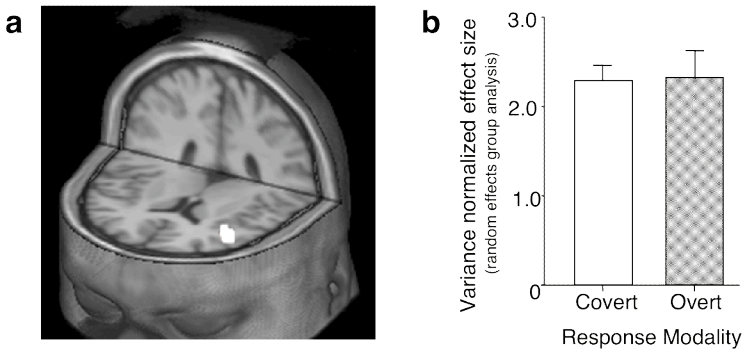

FIG. 3. (a) Activation in Broca's area during a picture naming task. (b) The magnitude of activation in this region was affected by picture-name agreement. Shown here is the magnitude of the name agreement effect in Broca's area during covert (unfilled) and overt (filled) picture naming.

Most relevant to the current discussion are studies we conducted examining the effects of competition during word retrieval both on activation in Broca's area in normal subjects and on performance in patients with focal lesions to Broca's area. During a word retrieval task, priming of irrelevant information was associated with increased activity in Broca's area (See Figure 2; Thompson-Schill et al., 1999). Similarly, Irene Kan and I recently asked subjects to retrieve the name of pictured objects that varied in name agreement (Kan & Thompson-Schill, 2004). As shown in Figure 3, we observed increased activity in Broca's area when subjects named pictures with low name agreement (e.g., a picture of a sofa, which was also called a couch, a loveseat, etc.) than those with high name agreement (e.g., a picture of an apple was uniformly called an apple). Both of these effects could reflect the response in Broca's area to increased demands for selection among competing representations. We tested the necessity of Broca's area for selection during word retrieval in patients with lesions to the left inferior frontal gyrus. Patients with lesions including Broca's area were impaired during word retrieval under high selection demands but unimpaired during word retrieval under low selection demands (Thompson-Schill et al., 1998). Furthermore, the degree of impairment was strongly correlated with the extent of damage in Broca's area (but not with overall lesion volume; see Figure 4). These observations demonstrate the necessity of Broca's area for selection among competing alternatives, in this case, during word retrieval.

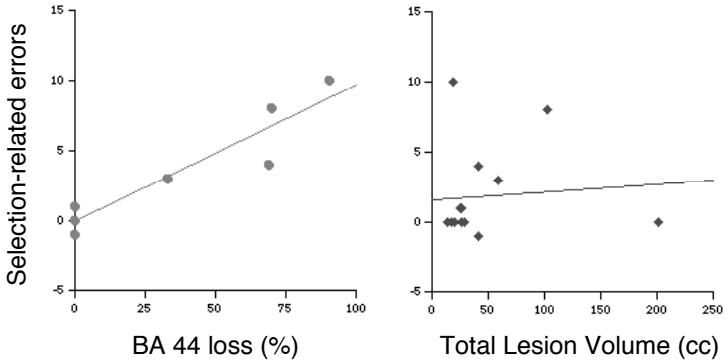

FIG. 4. Selection-related errors (high selection items – low selection items) on a word retrieval task, as a function of damage to pars opercularis (Brodmann's area 44; left panel; $r^2 = 0.91$) and as a function of overall lesion volume (right panel; $r^2 = 0.01$) in patients with focal, frontal lesions. Adapted from Thompson-Schill et al. (1998).

The Verbal Working Memory Organ?

The advent of neuroimaging has revealed many findings that were, in some cases, unanticipated by the neuropsychological literature. While it is easy to offer the widely repeated disclaimer "neuroimaging and neuropsychology address different problems", this avoids the question of why the two methodologies have not converged. One case of an apparent divergence in neuroimaging and neuropsychology is the study of working memory. Almost any neuroimaging paper on the topic of working memory will report activation in prefrontal cortex. In a recent review of neuroimaging studies, Cabeza and Nyberg (2000) noted activation in prefrontal cortex in all but 2 of 60 working memory comparisons (i.e., some condition requiring working memory compared to some baseline condition). In many of these comparisons, particularly with verbal tasks, activation was observed in Broca's area.

In contrast to the seemingly clear interpretation of these neuroimaging findings, a recent meta-analysis of neuropsychological studies of working memory showed that, in contrast to lesions in temporoparietal cortex, lesions to prefrontal cortex did not reliably lead to impairments in working memory capacity (D'Esposito & Postle, 1999). The authors suggested that frontal patients have deficits on working memory tasks that "require the mediation of other PFC-supported processes" (e.g., tasks with distractor-filled delay intervals; p. 1315). One such candidate process is selection: Activation in Broca's area is observed during working memory

trials in a proactive interference paradigm, in which probe familiarity is a competing source of information at response (Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998). We reported data from a patient with a lesion to Broca's area who had a selective impairment in his ability to inhibit proactive interference in working memory (see Figure 5; Thompson-Schill et al., 2002); we interpreted this deficit as a failure to select among competing sources of information. According to this account, activation in Broca's area might be observed during the delay period of working memory tasks as a precaution against potentially interfering stimuli; however, this activation would only prove to be necessary in working memory tasks where interference actually occurred. In other words, activation in Broca's area during working memory tasks is consistent with the hypothesis that the function of Broca's area is to guide selection when there are competing sources of information.

This hypothesis may have implications for a long-standing debate in the study of sentence comprehension: Do the tasks of assigning syntactic structure and interpreting the meaning of a sentence using that structure require a domain-specific separate-sentence-interpretation resource (e.g., Caplan & Waters, 1999) or do these tasks depend on a single verbal working memory capacity resource (e.g., Just & Carpenter, 1992)? We suggest that sentence comprehension depends on a resource that is better characterized as a non-mnemonic process than as a mnemonic capacity. That is, the single resource may be the ability to select between competing sources of information, which is necessary both for some working memory tasks and for some sentence processing tasks.

WHEN SELECTION FAILS: LANGUAGE PROCESSING WITHOUT BROCA'S AREA

The hypothesis that Broca's area subserves selection among competing sources of information was not developed in the domain of language *per se*. However, certain symptoms would be expected to arise from the operation of a language system that is unable to select between competing sources of information. These symptoms should be observed in patients with lesions affecting Broca's area. Notice that this does not lead to the hypothesis that all patients with a selection-impairment will have Broca's aphasia, nor does it lead to the hypothesis that all patients with Broca's aphasia will have a selection impairment. As reviewed above, there is neither a necessary nor sufficient relation between Broca's area lesions and Broca's aphasia; as such, this is not a hypothesis about Broca's aphasia *per se*. Rather, the claim is that certain *symptoms* should be observed in patients with damage to Broca's area

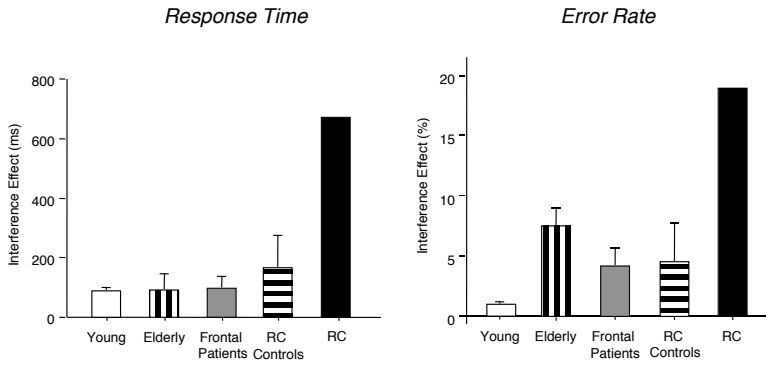

FIG. 5. A patient (RC) with left prefrontal damage including pars triangularis (Brodmann's area 45) showed an exaggerated interference effect in response time (left panel) and error rate (right panel) on working memory trials with recently-presented foils. Patients with frontal lesions sparing BA45 exhibited an interference effect comparable to age-matched control subjects. Adapted from Thompson-Schill et al., 2002.

as a result of an inability to select between competing sources of information. Although few experiments have explicitly tested this idea, here I review those findings that are consistent with this hypothesis, and outline a strategy for testing these ideas further.

Language Production

An impairment in word retrieval is a ubiquitous deficit in all types of aphasia and could result from failures at any stage in the word production process. In cases where a word retrieval failure is the result of a selection deficit, performance should be modulated by competition. Luria described the language production deficit associated with frontal lobe syndromes as "dynamic aphasia", reflecting that the linguistic deficits come and go as a function of context (Luria, 1973). Other investigators have reported that restricted lesions of Broca's area result in a syndrome that resembles transcortical motor aphasia, in which production impairments are primarily evident on generative language tasks such as verbal fluency or story-telling.

These types of deficits could result from a selection failure in unconstrained settings. There are several sources of experimental evidence that damage to prefrontal cortex (and in some cases, specifically to Broca's area) results in a word retrieval impairment that is best characterized as a failure to select among competing alternatives.

First, damage to prefrontal cortex is associated with selection-related impairments on verbal fluency tasks (e.g., retrieving the names of animals, or of words that start with F). A patient with a bilateral, frontal lesion was impaired at generating exemplars of the superordinate category "animals" but was normal at generating exemplars of the subordinate category "farm animals" (Randolph, Braun, Goldberg, & Chase, 1993). Presumably, the cue "farm animals" activates a more restricted set of representations, resulting in less competition among the set of candidate responses. Similarly, my colleagues and I reported that patients with early Alzheimer's disease (also associated with frontal dysfunction) were more impaired at generating words given a one-letter cue (e.g., words that start with "F") than at generating words given a two-letter cue (e.g., words that start with "FL"); in fact, one-third of the patients were able to produce more words in the latter case, again, presumably as a result of decreased competition among candidate responses (Tippett, Gendall, Farah, & Thompson-Schill, in press). The ability to initiate a switch between two semantic categories on a fluency task (e.g., from farm animals to jungle animals) has been linked to frontal lobe functioning (e.g., Troyer, Moscovitch, Winocur, Alexander, & Stuss, 1998); switching may require the inhibition of active (but already reported) representations using the same mechanisms required to override a prepotent response. Although selection in these cases has not been explicitly linked to Broca's area, these observations suggest a potentially fruitful line of future investigation.

Second, damage to prefrontal cortex is associated with selection-related word retrieval impairments on confrontation naming tasks (i.e., retrieving a word solely in response to a picture cue). In order to identify cases where confrontation naming fails as the result of a selection impairment, one would have to show that naming performance was affected by the number of competing alternatives. One way to experimentally introduce conflict among competing alternatives during confrontation naming is to present pictures in semantically-related blocks, which is known to exert an interfering effect in normal speakers (e.g., Damian, Vigliocco, & Levelt, 2001). An exacerbation of this interference effect was observed in a nonfluent aphasic patient with anterior damage (but critically, not in a patient with a posterior lesion) who exhibited a context-sensitive word-retrieval impairment that was interpreted as a failure of competitive selection (Wilshire & McCarthy, 2002).

The most detailed investigation of selection-related deficits in language production following damage to Broca's area comes from Robinson and colleagues (1998), who recently reported a case study of a patient with dynamic aphasia following a lesion of the left frontal operculum; this patient had an impairment confined to generative tasks with high selection demands. For example, when given a stem of a sentence and asked to generate a single word to complete it, the patient would fail with a sentence such as "Bob went to the store to buy some…" although she would succeed with "Bob takes his coffee with milk and …". In a second patient (Robinson, Shallice, & Cipolotti, in press), the selection deficit was confined to the language domain, indicating that the impairment was an inability to select between competing *verbal* representations.

Language Comprehension

As reviewed above, impairments in the syntactic analysis of sentences have been attributed to lesions of Broca's area; however, similar deficits have been observed in many types of aphasia (Dick et al., 2001), and among agrammatic Broca's aphasics, the pattern of deficits may vary (Badecker & Caramazza, 1985). Thus, we can ask (as above), what would a deficit in sentence comprehension caused by a selection impairment look like? Following from the idea that sentence interpretation involves a dynamic competition among multiple sources of information (e.g., Trueswell & Tanenhaus, 1994), we propose that selection demands are increased when these various sources do not converge on a unique interpretation (e.g., passive sentences, which pit syntactic and word order cues against each other). An inability to select between competing sources of information may have particular implications for syntactic cues, as some psycholinguists have argued that "a preliminary semantic interpretation is defined on an incomplete syntactic representation and is maintained unless inconsistent information arrives; thus syntax acts more like a filter for proposed interpretations" (Carlson & Tanenhaus, 1988, p. 286); patients with selection deficits may have an inability to "undo" these provisional interpretations (cf. Saffran, Schwartz, & Linebarger, 1998). In addition, this framework may explain why some patients with Broca's aphasia fail to comprehend simple sentences (e.g., active sentences; Schwartz, Saffran, & Marin, 1980), a phenomenon which has thus far been poorly explained by both syntactic theories (e.g., Grodzinsky, 1986) and limited resource theories (e.g., Dick et al., 2001). By our account, impairments might occur in comprehension of any sentence with competing interpretations, including reversible active sentences. At present, there has been no direct test of the claim that Broca's area is associated with selection-

related impairments in sentence comprehension; however, as many available data are consistent with this claim (e.g., Schwartz et al., 1980), it would be a potentially productive line of future investigation.

Another way to increase competition during sentence comprehension is to introduce ambiguity, either at the level of lexical (e.g., homonyms) or syntactic (e.g., garden path sentences) interpretation. Ambiguity that occurs when one word has two distinct meanings is a model case for understanding how semantic selection is necessary for normal language comprehension. For instance, in order to understand the sentence "He dug with a spade," the meaning of spade associated with shovel must be selected over the meaning associated with card games. Several studies have indicated that patients exhibiting symptoms of Broca's aphasia show a delay in selecting context-appropriate meanings of ambiguous words (e.g., Swaab, Brown, & Hagoort, 1998). More recently, the failure to select a context-appropriate interpretation has been linked to lesions of left prefrontal cortex (Metzler, 2001). Syntactic ambiguity resolution has not been investigated in brain-damaged patients, although the ability to resolve syntactically ambiguous sentences has been linked to working memory in normal subjects (MacDonald, Just, & Carpenter, 1992), and has been shown to be insensitive to context in young children (Trueswell, Sekerina, Hill, & Logrip, 1999), who often behave in a qualitatively similar way as patients with frontal lobe damage (e.g., Diamond & Doar, 1989). The investigation of these processes in patients with damage to Broca's area is the next logical step.

SUMMARY

As we approach the sesquicentennial of Broca's seminal paper, we have numerous hypotheses about the function (or functions) of Broca's area to consider and a slate of methods with which to do so. The proposal that Broca's area is involved in selecting information among competing sources of information provides a framework for studying both linguistic and non-linguistic deficits associated with damage to prefrontal cortex. This putative mechanism potentially relates to other hypotheses about language impairments, such as reduced lexical activation (Utman, Blumstein, & Sullivan, 2001), impaired contextual selection (Swaab et al., 1998), and even trace deletion hypotheses (see Zurif, 1995 for a discussion of the role of processing resources that sustain lexical activation during gap-filling). This mechanism may also play a role in unification operations linked to Broca's area (see Hagoort, this volume). In addition, the framework outlined here has the added advantage of continuity with other hypothesized functions of prefrontal cortex (e.g., Miller & Cohen, 2001) and thus with mechanisms that

can be studied in our pre-linguistic primate cousins. Returning briefly to the question of language evolution, it is tempting to note that both the communication of patients with lesions to Broca's area and the communication of nonhuman primates have been described as situation-specific (Jackendoff, 2002). The ability to select among competing sources of information may serve as example of "a trait present in nonhuman animals [that] did not evolve specifically for human language, although it may be part of the language faculty and play an intimate role in language processing" (Hauser et al., 2002, p. 1572). That is, perhaps the evolution of processes subserved by Broca's area was indeed critical for modern human communication, but not in the way that Broca initially envisioned.

ACKNOWLEDGEMENTS

The preparation of this article was supported by NIH R0160414, NIH R01067008, and the Searle Scholars Program. The following people contributed in meaningful ways to many of the ideas and experiments described here: Geoff Aguirre, Laura Barde, Laurel Buxbaum, Anjan Chatterjee, Branch Coslett, Mark D'Esposito, Lila Gleitman, Amishi Jha, John Jonides, Irene Kan, Dan Kimberg, Martha Farah, Bob Knight, Jared Novick, Tatiana Schnur, Myrna Schwartz, Geeta Shivde, Ed Smith, Marianna Stark, Diane Swick, and John Trueswell.

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