

Broca's Area and Language Processing: Evidence for the Cognitive Control Connection

Jared M. Novick^{1*}, John C. Trueswell² and Sharon L. Thompson-Schill²

¹University of Maryland, College Park and ²University of Pennsylvania

Abstract

A long-standing pursuit in cognitive neuropsychology has been to understand the role of Broca's area in language processing. Although a prevailing view has been to equate this region with grammatical abilities in both production and comprehension, a host of recent evidence from brain imaging and patient research has revealed a rather general role for this patch of cortex in complex cognition, even when grammatical performance is untapped—namely, that it regulates mental activity when there is need to resolve among competing representations. In this light, a recent proposal hypothesizes that this broad 'cognitive control' function of Broca's area similarly serves language processing: Broca's area is responsible for biasing production and comprehension processes when there are strong demands to resolve competition among incompatible characterizations of linguistic stimuli. Some questions that have been asked within this framework are as follows: Does Broca's area help speakers produce an appropriate word when many alternatives are equally plausible? Does it permit readers and listeners to successfully understand words and sentences, even when the input is ripe for misinterpretation? In the current article, we review new empirical evidence from various fields that supports such an account. A central piece to this discussion is how careful scrutiny of language performance, under varying degrees of cognitive control demands, may shed light on how to suitably describe the idiosyncratic language traits of patients with focal Broca's area damage, who are decidedly not agrammatic.

When explaining how he drives home every weekend, Patient A says:

"Why, yes ... Thursday, er, er, er, no, er, Friday...Bar- ba - ra...wife...and, oh, car... drive... purn-pike...you know... rest and...TV." (Gardner 1975, p. 61)

When discussing several electronic Christmas tree ornaments, Patient B says:

"That one, every time you go by, it sings."

Introduction

The two exchanges above come from two very different patients studied in the field of neurolinguistics. The first patient's speech can be characterized by frequent interruptions and dysfluencies, and it contains little or no syntactic coherence. The second patient, by contrast, produces an intelligible, syntactically complex sentence, which contains a noun phrase modified by a relative clause (*every time you go by*), and even uses the syntactically acrobatic maneuver of contrastive topicalization. In classic terms, then, Patient A demonstrates the representative profile of an agrammatic Broca's aphasic; Patient B quite obviously does not. Thus, one might be surprised to learn that Patient B has a documented focal lesion to Broca's area (Novick et al. 2009). Patient A may or may not have damage there, because anatomical reports are not typically part of the clinical information used to

diagnose aphasia. What should be clear, however, is that injury to Broca's area is neither necessary nor sufficient to bring about the putative linguistic impairments associated with this well-known disorder (a fact that has been detailed more methodically elsewhere, e.g., Alexander et al. 1990; Dick et al. 2001; Dronkers 2000a,b).

This is not to say, of course, that because Patient B's syntactic abilities are relatively intact, he is necessarily free of language impairment altogether. Although there are no reported cases documenting that patients who have brain damage similar to B's (i.e., restricted Broca's area damage) suffer from the full symptom complex of Broca's aphasia, one common symptom this population does exhibit is an emblematic lack of verbal fluency under some, but not all, conditions. Luria (1973) referred to this deficit as 'dynamic aphasia', because such production difficulties emerge more obviously at certain times versus others. But when? Generally speaking, it has been difficult to systematically describe under *what* conditions exactly these patients' language deficits actually arise. Why is their production seemingly so normal in some cases, but abnormal in others? What are the specific circumstances under which their production is impaired? Is their ability to comprehend language similarly evanescent, also marked by characteristically preserved grammatical skills? In view of these curiosities, researchers have been scrutinizing the explicit makeup of this population's general cognitive profile, including linguistic and non-linguistic abilities, to better inform their understanding of these patients' distinctive language traits. In addition, researchers use functional neuroimaging methods to study the role of Broca's area in complex cognition within healthy adults as they complete a range of tasks, including language processing.

Considering findings from recent years, various investigators have begun proposing a connection between Broca's area – specifically the posterior region of the left inferior frontal gyrus (Brodmann areas 44 & 45; hereafter LIFG) – and cognitive control (e.g., Nelson et al. 2003; Badre and Wagner 2007). Cognitive control refers to the mental ability to guide and adjust one's attention and actions in accordance with current goals. For example, consider an American pedestrian in London: using cognitive control, she must rein in her dominant bias to look left first before crossing the street. In the laboratory, the prototypical example of such prepotent response conflict comes from the Stroop task: naming the ink color of printed color words involves cognitive control because the instruction to attend to the perceptual stimulus conflicts with the well learned response to read the word; it is hard to utter 'blue' when the word *red* appears in blue font. When individuals override such highly regularized or automatic behaviors, Broca's area within LIFG is recruited to promote a normally disfavored but presently appropriate response, in lieu of the most dominant one that initially comes to mind (for variants of this task, see Carter et al. 2000; Mead et al. 2002; Milham et al. 2003; January et al. 2009).

As sketched briefly in the following section, the finding that LIFG is active in cases of cognitive control has been documented across a wide variety of experimental paradigms. By and large, LIFG appears to be involved when individuals must resolve conflicting information about how to characterize a stimulus, or how best to respond to that stimulus; this is found even for tasks requiring little or no syntactic processing. Nevertheless, such a pattern of results may be quite informative about the role Broca's area plays in language processing, namely, it might serve the very same cognitive control function observed in more general cognitive tasks. By decomposing the processes that are believed to support online language processing, Novick et al. recently identified several predictions about the specific circumstances under which LIFG should engage to support production and comprehension (Novick et al. 2005). This includes ways to more aptly characterize the nature of the cognitive and language impairments suffered by individuals like Patient

B. In the current article, we review the evidence that has accumulated in recent years, since the publication of Novick et al. 2005, in support of the cognitive control and language processing theory.

Broca's Area and Cognitive Control

For over a half century, the prefrontal cortex (PFC; see Figure 1) has been associated with goal-directed, flexible behavior, including the ability to adapt to new rules and frequent changes in task demands (see Miller and Cohen 2001 for a review). The function of PFC has been characterized as one of dynamic filtering (Shimamura 2000) or 'sculpting the response space' (Fletcher et al. 2000), by selecting appropriate and inhibiting inappropriate information. More recently, researchers have started to divide the PFC into functional-anatomical components, to more clearly delineate which regions within PFC support specific sorts of cognitive control function.

The LIFG's connection to cognitive control has been documented across several brain-imaging studies that have employed a wide array of experimental tasks that manipulate cognitive control demands. As introduced earlier, conflict-related trials on the Stroop task routinely give rise to LIFG activity, reflecting the need to override the prepotent reading response in favor of naming the color-terms' ink color (e.g., Milham et al. 2003). Further evidence comes from other conflict-related paradigms such as flanker tasks, in which participants respond to a centrally displayed stimulus (e.g., the direction of an arrow) that is surrounded by competing stimuli (e.g., arrows pointing in the opposite direction; e.g., Van Veen et al. 2001; Ye and Zhou 2009).

Rather than thinking simply about 'cognitive control tasks' (like the Stroop task), it has been increasingly useful to try to vary the demands for cognitive control within a wide range of tasks and to observe the consequences of these subtle manipulations. One of the first examples of this approach arose from an attempt to understand the role of prefrontal cortex in working memory: Jonides et al. modified a verbal working memory paradigm to manipulate proactive interference (PI) and, therefore, demands for cognitive control (Jonides et al. 1998; see Monsell 1978). In this task, participants had to respond to a probe letter (e.g., D) by indicating whether it appeared in an immediately preceding memory set (e.g., s f d m). On most trials, participants could rely on stimulus familiarity to accurately judge whether the correct response was yes or no. However, on a small

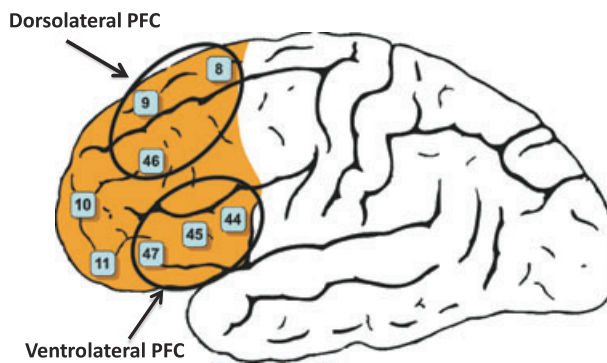


Fig 1. Schematic lateral view of the brain's left hemisphere. The prefrontal cortex (PFC) is shaded orange. Number labels indicate Brodmann areas (BAs). The left inferior frontal gyrus (LIFG) falls within ventrolateral portions of PFC, including the posterior anatomical regions known as Broca's area (BAs 44 & 45).

subset of 'no' trials, characterizing a probe letter on the basis of familiarity alone was susceptible to error. This is because on such trials, the probe letter (e.g., H) did not appear in the current memory set (e.g., k p w n) – so the correct response was no – but it did appear on the previous trial (e.g., h l w p). Thus, there was some remaining and persistent familiarity of the probe due to its recent appearance. Participants therefore needed to defy their reliable familiarity bias, because it would have guided them toward an incorrect 'yes' response; they instead had to attend to the foremost activation of letters from the current memory set and re-characterize the probe stimulus as 'familiar-but-outdated', thereby indicating a 'no' response. Relative to 'non-recent-no' trials, in which the probe letter did not appear on the current or prior trial, reaction times and error rates on these 'recent-no' trials increase significantly. And this contrast routinely boosted LIFG activity (see also Nelson et al. 2003; Jonides and Nee 2006). Thus, the similar pattern of activity for this and the Stroop task is hypothesized to be the result of a common need to override highly routinized but currently incorrect ways of representing a stimulus that might cause a flawed response.

We highlight the PI task in particular because, across three separate case studies testing patients with circumscribed LIFG lesions, the patients' PI effect is greatly exaggerated. That is, they exhibit especially high error rates (and in some cases reaction times), well outside the normal range, for recent-no trials versus non-recent-no trials when compared to healthy individuals and other frontal patients whose LIFG is undamaged (Thompson-Schill et al. 2002; Hamilton and Martin 2005; Novick et al. 2009). One of these cases (ML; see Hamilton and Martin 2005) was also tested on the Stroop paradigm, and was similarly impaired under incongruent conditions. And indeed, Patient B (also known as IG in the published literature—initials we will adopt hereafter; see Novick et al. 2009), whom we introduced earlier, is another of the patients showing such an exaggerated PI effect. Later in this paper, we revisit Patient IG to discuss how this general cognitive control impairment affects his language processing.

Taken together, these patient studies, alongside the neuroimaging findings described above, have led several researchers to conclude that there is a consistent link between cognitive control and LIFG. Further, these studies demonstrate that cognitive control is required beyond measures that have been classically associated with dysexecutive syndromes, such as Stroop, go/no-go tasks, and so on; thus the involvement of LIFG can depend on what appears to be fairly subtle variations of any number of tasks.

Indeed, besides the PI task, researchers have delicately manipulated cognitive control demands within other paradigms—that are not classically known as cognitive control tasks per se—and have observed increased LIFG recruitment under high versus low demands for control. Some examples include verb generation tasks (Thompson-Schill et al. 1997), picture-naming tasks (e.g., Kan and Thompson-Schill 2004; Schnur et al. 2009), lexical decision tasks (e.g., Grindrod et al. 2008), and phonological or semantic judgment tasks (e.g., Snyder et al. 2007). The need for cognitive control in these tasks depends on the presence of 'conflict' in the designs. The term 'conflict' denotes instances in which current situation-specific demands give rise to an incongruity between how a stimulus should be represented or responded to, in view of how the stimulus is ordinarily characterized (think of Stroop). This type of conflict is referred to as 'prepotent response conflict', because individuals must override their dominant (prepotent) biases in favor of disfavored alternatives (see Botvinick et al. 2001). Similarly, conflict can arise in the form of 'under-determined response conflict', in which multiple response candidates are equally plausible and therefore compete for selection (Botvinick et al. 2001). For instance, in the verb generation task, participants produce verbs that are associated with the nouns they are given.

Some nouns have many associated verbs (high competition; e.g., ball → kick, throw, catch), whereas others have only one strongly associated verb (low competition; e.g., scissors → cut). Resolving both types of conflict—i.e., prepotent response conflict and underdetermined response conflict—requires top-down regulatory control (Botvinick et al. 2001).

Elsewhere, we have argued that there should be a specific connection between such cognitive control abilities and our ability to comprehend language (Novick et al. 2005). While reading or interpreting speech, for example, we rely on the build-up of syntactic and semantic evidence to guide us toward an interpretation, and, along the way, we make our ‘best-guess’ estimate about what is likely to come next (see Pickering and Van Gompel 2006; Tanenhaus 2007; Trueswell and Gleitman 2007). But sometimes these accumulating evidential sources lead us astray; one fallout of incremental processing is that the first analysis we assign occasionally turns out wrong (the so-called ‘garden-path’ effect in psycholinguistics). When this happens, we must revise our initial analysis and recover an alternative. Novick et al. (2005) hypothesized that the discovery of a misinterpretation triggers the need for cognitive control processes to help resolve the conflict between two incompatible representations of sentence meaning: the one we originally assigned and the one we must recover, akin to the prepotent and controlled processes needed to resolve conflict in the Stroop and PI tasks. Likewise, during production, lexical access involves resolving competition: words compete with each other for selection. Competition might be especially fierce when multiple semantically related words are equally plausible candidates for production.

If comprehension and production under conditions of conflict are modulated by general cognitive control abilities, like those governing conflict resolution on Stroop- and PI-like tasks, then LIFG should be involved to implement control to avoid processing errors (a misinterpretation; uttering the wrong word). That is, Broca’s area might re-organize parsing patterns during comprehension, or bias selection of one candidate response over another during production. Can this explain the types of language impairment LIFG patients (like IG) suffer from, who are otherwise syntactically intact (i.e., not agrammatic)? We will address this in future sections.

Neuroimaging Evidence that Similar Cognitive Control Processes are at Work in Real-Time Language Comprehension

What might count as evidence for common processing across cognitive control tasks? At first blush, there would seem to be ample support for a shared mechanism from the neuroimaging literature, which contains reports of LIFG activation across many different tasks, including language tasks. However, this conclusion would be premature. Broca’s area within LIFG is a relatively large region, and includes several anatomically distinct areas (e.g., dorsal and ventral regions within BAs 44 and 45) (Amunts et al. 1999). It turns out, however, that these areas differ considerably from person to person, in that the size, location, and shape of BA 44 and 45 are usually quite different across brains (Tomaiuolo et al. 1999). Given such variability, several labs have begun to argue that group analyses of neuroimaging data may be inappropriate because activations are analyzed in a standardized, common-brain space, thereby obscuring a clear understanding of functional-anatomical specificity (e.g., Derrfuss and Mar 2009; Derrfuss et al. 2009; Fedorenko and Kanwisher 2009). This suggests the importance of alternative methods, including within-individual analyses of activation, and task-to-task co-localization in each participant’s brain to evince more dependable patterns.

Perhaps, then, the most compelling evidence supporting the cognitive control and language processing account comes from two brain-imaging studies that tested for within-individual co-localization of LIFG activity across syntactic and non-syntactic conflict resolution tasks (January et al. 2009; Ye and Zhou 2009). Both studies examined comprehension, but differed in modality. In January et al. (2009), participants completed two tasks while undergoing fMRI: a Stroop task and a spoken comprehension task that involved listening to ambiguous sentences. Specifically, participants heard sentences like *Clean the pig with the leaf*, which contained a prepositional phrase (PP)—e.g., ‘with the leaf—that could indicate an instrument with which to carry out an action, or denote a modifier that identified which object to act on. The authors manipulated the type of scene that listeners saw while hearing the sentences, to vary contextual support for each interpretation. For example, in the condition containing the most conflict, there would be a picture of a toy pig holding a leaf next to a sponge, which is a good cleaning instrument. In such a case, the authors hypothesized that cognitive control should be involved to bias activation away from the instrument reading of ‘with the leaf’. In another condition, the sponge was replaced with a rock (a bad cleaning instrument), so the scene clearly supported the modifier analysis of the ambiguous PP; consequently there was less conflict between the PP and the referential context. In a third condition, the instruction unambiguously referred to a modifier (*Clean the pig that has the leaf*).

The authors defined two regions of interest in LIFG for each participant, one for the Stroop-incongruence effect (incongruent minus congruent trials) and another for the ambiguity effect. Each contrast evoked a strikingly similar pattern of activation *within individuals*. That is, the Stroop and parsing conflict effects co-localized in Broca's area (BA 44/45): compared to unambiguous sentences containing no conflict, sentences that created the greatest conflict between two alternatives of sentence meaning (e.g., ‘with the leaf’ as instrument versus modifier in the presence of a potential cleaning instrument, e.g., a sponge) showed higher activation in the *Stroop* ROI. And incongruent Stroop trials (e.g., the word *red* printed in blue ink) showed higher activation compared to neutral trials (e.g., the word *red* printed in red ink), in the *Ambiguity* ROI. Because completing the Stroop task does not involve sophisticated syntactic processes, the authors concluded that LIFG underlies a general conflict resolution mechanism that is shared by many task types; in the case of parsing, it deploys when there is need to resolve conflict between multiple opposing representations of sentence meaning.

January et al. also manipulated referential ambiguity in the study to gauge the extent of the conflict resolution mechanism. Interestingly, they did not observe increased activation in LIFG in response to increased referential conflict. In the strongest case of referential conflict, two toy animals of the same type (e.g., two pigs) were displayed holding different objects (e.g., one with a rock, the other with a leaf), while participants heard syntactically unambiguous instructions like *Clean the pig that has the leaf*. Thus, either animal could have been the intended referent until the very end of the sentence. This case was compared to weaker forms of referential ambiguity, namely when the second pig was holding nothing, such that the correct referent could be identified earlier (i.e., upon hearing *Clean the pig that has...*). Despite the authors' failure to find LIFG activation in response to increasing levels of referential conflict, they cautioned that it would be premature to conclude that referential conflict resolution does not trigger the same control mechanisms as syntactic- and Stroop-related conflict. First, the authors acknowledge that this manipulation may have been weaker than the syntactic or Stroop manipulations. Second, and perhaps more relevant, the authors performed a post hoc analysis on some of the non-target filler sentences, which contained *global* (rather than *temporary*) referential

ambiguities. In so doing, they did observe LIFG activation in the original ROIs. In other words, in extreme cases of referential conflict, when neither the linguistic input nor the context resolved the ambiguity (e.g., *Pat the dog*, when there were two toy dogs present), LIFG was recruited significantly more than any other level of referential conflict in the experimental manipulation. Nevertheless, these filler items were few in number and activated a smaller number of voxels than the syntactic conflict comparison. Consequently, the authors' conclusions remain tentative concerning whether referential conflict recruits the same or different mechanisms as syntactic and Stroop conflict.

Another group of researchers (Ye and Zhou 2009) have reported a strikingly similar co-localization finding in the reading domain, adding to January et al. spoken comprehension result. In their study, Ye and Zhou had participants complete three tasks while in the scanner: two non-parsing conflict resolution tasks, flanker and Stroop, and a parsing task that involved reading sentences with conflict between two potential but incompatible interpretations—one guided by the input's active syntactic construction and the other by its thematic roles (cf. *The policeman kept the thief in the station* [Plausible/No-Conflict] versus *The thief kept the policeman in the station* [Implausible/Conflict]). In implausible conditions, the subject noun phrase ('The thief...') was more compatible with a passive structure (*The thief was kept by the policeman...*); thus, the active construction conflicted with the expectation the propositional content engendered. The Plausibility contrast elicited greater LIFG activity, that is, when the syntax and semantics competed for a coherent interpretation. Alongside this effect, the Stroop- and flanker-incongruence effects (incongruent minus congruent trials) also consistently activated LIFG. As a whole, the authors reasoned that domain-general cognitive control processes exert their influence to resolve conflict during sentence processing, and that LIFG is a candidate region that supports such a shared mechanism. This finding further bolsters support for the hypothesis that the role of LIFG in language is not syntax-specific, but that its role in syntactic tasks is to resolve conflict between temporarily incompatible representations.

Using similar materials, Ye and Zhou (2008) also reported findings from an event related potential (ERP) study in which participants were first divided into high- versus low-cognitive control ability as indexed by their Stroop performance. This grouping factor predicted variations in both ERP patterns for the plausibility contrast, and the degree of processing difficulty readers experienced. Further, patterns of ERP activity reliably predicted the size of individuals' Stroop-incongruence effects. These correspondences suggest that cognitive control mechanisms are involved in recovering from misinterpretation when readers must resolve conflict between incompatible representations of sentence meaning. Additional analyses revealed that general processing speed and working memory capacity could not account for these effects. Overall, the results strongly imply that individual differences in parsing abilities—especially concerning reanalysis—can be captured by normal variation in cognitive control function.

Taken together, LIFG is responsive to conflict resolution processes in both parsing and non-parsing paradigms, even when co-localized within individual brains. Co-localization in LIFG across tasks suggests that general cognitive control functions are shared by the parsing system, and are manifest when readers or listeners must resolve among multiple incompatible representations. That variation in cognitive control and parsing functions are both modulated by LIFG in healthy adults raises the following question: in extreme populations, like young children and patients with LIFG damage, can radical disparities in cognitive control ability, compared to healthy adults, capture dramatic differences in language processing performance? We discuss these extreme groups in sequence.

Developmental Research

Although adults are known to experience temporary difficulty with garden-path sentences (e.g., Ferreira and Henderson 1990, 1991; Garnsey et al. 1997; Novick et al. 2008; Tanenhaus et al. 1995; Trueswell et al. 1999; *inter alia*), they are nevertheless quite skilled at recovering the correct meaning of such sentences. Adults can exert rapid control over interpretive processes, inhibiting hypotheses proven incorrect and promoting hypotheses consistent with newer input. Children, by contrast, might be expected to have difficulty executing such processes, because developmental changes in cognitive control are known to occur throughout childhood (Davidson et al. 2006; Diamond et al. 2002; Müller et al. 2005). For instance, preschool-aged children frequently show deficits in tasks when they tap into inhibitory control, such as the Go/No-Go task (Durstun et al. 2002), the Stroop task (Bub et al. 2006; Prevor and Diamond 2005), and other related tasks (Carlson and Moses 2001; Carlson et al. 2002; Davidson et al. 2006; Sabbagh et al. 2006). In most cases, it is not until adolescence that children begin to show adult-like efficiency in over-riding prepotent/automatic responses to stimuli (Anderson et al. 2001; Anderson 2002; Diamond et al. 2002). It is widely believed that this protracted developmental profile is connected to the protracted neurodevelopment of frontal lobe brain regions (Huttenlocher and Dabholkar 1997; see also Mazuka et al. 2009).

As noted by Novick et al. (2005), these developmental changes in cognitive control abilities predict that younger children might not deal well with garden-path sentences, which require inhibiting an initial prepotent interpretation. Indeed, such developmental changes have been observed (e.g., Trueswell et al. 1999; see Hurewitz et al. 2001; Kidd and Bavin 2005; Weighall 2008). In one study, Trueswell et al. (1999) recorded the eye movements and actions of 5-year-olds, 8-year-olds, and adults, as they responded to spoken instructions to move toy animals on a table. This method, often referred to as the 'visual-world' paradigm, provides a moment-by-moment record of listeners' real-time interpretive commitments by recording their eye fixations on objects as they listen to each instruction. On the trials of interest, participants heard an instruction ripe for misinterpretation because it began with a highly biased temporary syntactic ambiguity, as in:

1. Put the frog on the napkin into the box.

The first PP, *on the napkin*, is technically ambiguous; it could be a Destination phrase for the verb *put* (i.e., telling the listener where the frog should go) or a Modifier for the Noun Phrase (NP) *the frog* (i.e., telling the listener more about the frog). All age groups had a strong preference to initially interpret this ambiguous phrase as a Destination. In a scene containing a frog sitting on a napkin, an empty napkin, and an empty box, hearing 'Put the frog...' generated rapid eye movements to the frog, and hearing 'on the napkin' generated increased looks to the empty napkin; this latter eye movement pattern suggested that listeners were considering this as a possible Destination to move the frog to. Upon hearing 'into the box', however, clear age differences emerged. Older children and adults showed some signs of processing difficulty, looking around the scene, but eventually moved their eyes back to the frog; they then picked it up, and moved it into the box. Such a pattern suggests that they revised their parsing commitment from a Destination to a Modifier. Five-year-olds, in contrast, showed signs of an inability to revise this initial Destination interpretation. On about 60% of trials, children made errors in their actions, such as moving the frog first to the empty napkin, and then into the empty box. Strikingly, all errors for temporarily ambiguous instructions involved moving an object to

the Incorrect Destination, suggesting that they were honoring the Destination analysis of *on the napkin*. Together, these data suggest that younger children formed an initial Destination interpretation of the ambiguous phrase based on the verb *Put* (that it requires a destination to be provided) and had difficulty revising this commitment even after encountering countervailing linguistic evidence (*into the box*), with this difficulty perhaps being due to their immature cognitive control abilities.

In recent years, there have been several replications of the Trueswell et al. (1999) developmental finding that children often fail to revise parsing commitments (e.g., Hurewitz et al. 2001; Weighall 2008). Perhaps most notable for the current discussion, this observation has also been made for children learning other languages (Choi and Trueswell 2010). In this study, Korean-speaking 5-year-olds failed to recover from garden-path sentences. The striking aspect of the experiment, however, was that Korean is a verb-final language: verbs come at the end of sentences rather than at the beginning (as they do in English instructions like above). Even though verbs are highly informative cues to sentence structure, Korean children were shown to be reluctant to use verb information to override parsing decisions made regarding earlier phrases in the spoken instruction (based on case-marker information, see Choi and Trueswell 2010). Both eye movements and actions indicated that they initially pursued a particular interpretation and failed to revise that interpretation in the face of a verb that required a different analysis.

Importantly, the normal developmental delays in cognitive control abilities have been found to impact directly other aspects of language comprehension. Nilsen and Graham (2009) had children ages 3–5 participate in a referential communication task, in which they were talking with an adult about objects present in front of them. Some objects were jointly visible to both individuals (common-ground objects) whereas some were visible only to the child (privileged-ground objects). On critical trials, the adult uttered a request that was only ambiguous if the child had not taken into account the common-ground/privileged-ground status of the objects, e.g., ‘Hand me the duck’, when one duck was in common ground and the other was in privileged ground. Children’s ability to avoid visual consideration of the privileged-ground referent (and even to avoid picking it up) was highly correlated with their cognitive control abilities, as assessed by Stroop-like tasks that children also completed. This connection suggests that children in this age range can take into account the speaker’s perspective (and indeed want to) but that they have trouble using this information accurately because of late developing inhibitory control mechanisms. A very similar pattern has been observed in children’s use of context to resolve ambiguity related to word meaning (Khanna and Boland 2010). In that study, the authors observed that differences in children’s performance on a general cognitive control task (the go/no-go task) was positively correlated with their ability to rapidly promote contextually appropriate meanings of ambiguous words and inhibit inappropriate meanings (see Mazuka et al. 2009, for further examples of relationships in children between cognitive control and language processing; see Brown-Schmidt 2009, for a corresponding finding in adults).

Neuropsychological Case Studies of Patients with Circumscribed LIFG Damage

Our interpretation of the brain imaging and developmental findings reviewed above is further supported by convergent results from cognitive neuropsychology; recent work studying the language abilities of patients with focal lesions to LIFG, like Patient IG, has begun to characterize the nature of these patients’ linguistic deficits in general conflict resolution terms. Under the cognitive control account, damage to LIFG is hypothesized

to yield a general cognitive deficit in conflict resolution abilities; this in turn makes specific predictions regarding the language production and comprehension impairments that follow a more general failure of cognitive control. In particular, when conceptual, lexical, syntactic, or semantic representations compete for a response, thereby creating high conflict resolution demands, patients with circumscribed lesions to LIFG should have particular difficulty resolving the conflict. Consequently, production and comprehension should suffer but only under these particular circumstances. We begin with a review of some recent findings in production that support this account.

Production

As mentioned earlier, using the modified letter recognition task, Novick et al. (2009) demonstrated a general cognitive control deficit in Patient IG, reflected by an inflated proactive interference effect. This finding replicated two previous case studies of patients with similar lesion contours (Thompson-Schill et al. 2002; Hamilton and Martin 2005). On the basis of IG's abnormal cognitive control profile, like other LIFG patients (Thompson-Schill et al. 2002; Hamilton and Martin 2005), Novick et al. made predictions about his production and comprehension abilities under conditions of high versus low conflict resolution demands.

Novick et al. (2009) tested IG's production abilities across two tasks and compared them to healthy controls and other frontal patients whose injury did not impinge on LIFG. First, on a confrontation picture-naming task, participants were asked to name pictures of common objects. Pictures that could be associated with multiple possible names (i.e., low name agreement), such as a drawing of a piece of furniture that might be called a couch, a sofa, or a loveseat, were hypothesized to present acute difficulty for IG because all the name options, generated by their conceptual representations, should compete. Moreover, no name option was any more or less plausible than the others. Thus, competition demands were relatively strong in such cases compared to pictured objects that had high name agreement, such as an apple. High-name-agreement items were hypothesized to present no naming difficulty, as the conflict demands were relatively constrained. The researchers chose this task partly because in a prior fMRI experiment studying healthy adults, a low- minus high-name-agreement contrast resulted in increased LIFG activity (Kan and Thompson-Schill 2004). Indeed, in the patient study, when the to-be-named images had low name agreement—and thus high conflict demands owing to multiple possible candidate responses—IG committed errors marked by either a failure to respond entirely, or by uttering the basic level category name (e.g., 'furniture'), which no healthy adult did. Such an error rate fell well outside the control group's range of performance. Moreover, no other patient demonstrated this pattern. When IG had to name, by contrast, objects with high-name agreement and therefore fewer alternative labels (apple), IG's production was indistinguishable from that of healthy adults.

In a second production experiment, participants generated as many exemplars as possible for a given superordinate category (e.g., Animals), or, in a separate testing session a few weeks later, a corresponding subordinate category (e.g., Farm Animals). When category set size was large and relatively unconstrained (e.g., Animals), compared to smaller categories with a comparatively more restricted set of exemplars (e.g., Farm Animals), IG was unable to use the larger categories to produce a greater number of category members, unlike healthy controls. Whereas healthy participants produced more exemplars given a larger pool of possible responses (i.e., in the superordinate categories) than when there was a smaller pool of possible responses (i.e., in the subordinate categories), the difference

in the number of exemplars IG produced between the two conditions was significantly smaller. These data support the claim that LIFG is necessary to guide semantic retrieval when stimulus cues do not sufficiently constrain the response. Alongside the name agreement experiment, IG's production suffered when stimulus cues did not amply confine a single response.

In light of IG's significantly increased PI effect on the letter recognition task, Novick et al. (2009) characterized his production abilities in broad conflict resolution terms: irrespective of task-type, IG exhibited difficulty producing spoken words when multiple candidate options competed on a lexical-semantic level. By contrast, under conditions of reduced competition, IG's production was normal. Such a finding begins to explain the dynamics of Luria's observation—that is, the rise and fall of production difficulty appears to be tied to general conflict resolution and cognitive control abilities.

These results converge with a host of findings from Robinson et al. (1998, 2005). For instance, in one study, an LIFG patient, ANG, was tested on sentence completion tasks in which initial sentence fragments permitted multiple underdetermined possible continuations (e.g., an open-ended context such as *The man entered his house and...*). On such trials, ANG demonstrated an acute failure to complete the fragment relative to conditions in which the number of possible continuations was more constrained (e.g., *The man entered the cinema and...*, where comparatively fewer plausible continuations exist, like *watched a film*). The authors reasoned that the unconstrained conditions provided too many competing alternative continuations for ANG to resolve; thus ANG's damage to Broca's area resulted in 'an inability to select a verbal response in situations where the stimulus activate[s] many competing response options' (Robinson et al. 1998; p. 82). In another study, Robinson et al. (2005) reported the results of several verbal and non-verbal tasks completed by patient CH, another dynamic aphasic who, similar to ANG, had a fairly circumscribed lesion in LIFG. CH exhibited a conspicuous failure to produce language when multiple possible responses were activated by a stimulus and therefore competed for selection, on tasks akin to those IG completed, and to those ANG completed, among others. And the authors demonstrated that the patient's deficit was confined to the verbal domain; that is, CH had difficulty at the levels of word and sentence production under conditions of competing response options, but this pattern did not complement a more general impairment to generate responses overall—CH exhibited normal patterns in a range of motor and gesture fluency tasks under various conflict demands.

Lastly, Schnur et al. (2009) recently reported a study in which 12 patients with LIFG damage completed a picture-naming task in which cognitive control demands were manipulated within-item (in contrast to the name agreement manipulation described above, which is implemented across-items). In this task, objects appear repeatedly across naming cycles in either semantically homogeneous blocks (e.g., snake, cow, dog, ant) or semantically heterogeneous blocks (e.g., snake, bus, axe, chair). Generally, healthy speakers take longer to produce names of pictures in homogeneous contexts when compared to mixed contexts due to the increase in lexical-semantic competition among semantically related competitors (e.g., Hodgson et al. 2003; Belke et al. 2005). In an earlier study of this blocking effect in aphasic speakers (Schnur et al. 2006), some patients showed atypically large effects of semantic competition; in Schnur et al. (2009), these effects were directly related to the location of brain damage on a voxel-by-voxel basis. Indeed, the greater damage within the LIFG – in particular to one region of dorsal 44 – was associated with greater errors after repeated naming of semantic competitors. In other words, LIFG patients' 'ability to resolve competition that arises in the course of language processing appears to depend on the integrity of the LIFG' (Schnur et al. 2009; p. 324). Interestingly,

this finding was complemented by an fMRI study of healthy individuals completing the blocked-cycle naming paradigm. The homogenous minus heterogeneous contrast yielded increased LIFG activity; further, healthy adults with a greater LIFG response to semantic blocking were apt to make more naming errors in the homogenous condition when compared to those with less LIFG activation.

Overall, the following picture emerges for patients with focal LIFG damage: their production cannot be characterized by unmitigated dysfluencies under all production attempts; rather, their difficulty ebbs and flows. In view of the mounting evidence reviewed above, it appears that their language production is sensitive to how many competing lexical or conceptual alternatives there are; difficulty arises when competition demands reach a relative peak. Indeed, such difficulty can be tied to general conflict resolution and cognitive control abilities, as demonstrated in patient IG. In what follows, we briefly address the question we posed in the introduction: are these patients' comprehension abilities similarly fleeting, materializing only when conflict resolution and cognitive control processes are vital?

Comprehension

Returning again to IG, Novick et al. (2009) recently demonstrated that his general cognitive control impairment predicts specific language comprehension deficits alongside his conflict-related production difficulty. Comprehension was tested using the same visual-world *Put* study reviewed above for children (see also Tanenhaus et al. 1995; Spivey et al. 2002; Novick et al. 2008) to test, in part, if IG also failed to recover from temporary misinterpretation like 5-year-olds—a population with suboptimal cognitive control performance as a result of undeveloped prefrontal systems (see references above). The results were markedly similar to those found for the various groups in the Trueswell et al. (1999) study. All participants—including IG, frontal patients with LIFG intact, and age-matched controls—had a strong preference to initially interpret the ambiguous phrase, *on the napkin*, as a Destination. Hearing 'Put the frog...' elicited swift eye movements to the frog, and hearing 'on the napkin' elicited increased looks to the empty napkin, which again suggests that listeners were considering this as a potential Destination for where to move the frog. Upon hearing 'into the box', however, IG's patterns were noticeably different from the comparison groups. Healthy adults and frontal patients with an intact LIFG showed some signs of processing difficulty, but eventually moved their eyes back to the frog; they then picked it up, and moved it into the box. Said another way, they revised their parsing commitment from a Destination to a Modifier. IG, on the other hand, exhibited extreme difficulty revising this initial Destination interpretation—he dwelled on the empty napkin for an unusually (and highly significant) long time. Moreover, like 5-year-olds, IG made errors in his actions on over 60% of ambiguous trials: he first moved the frog to the empty napkin, and then either left it there, or put it into the box. Thus, like young children, all of IG's errors for temporarily ambiguous instructions involved moving an object to the incorrect destination, suggesting he was sticking to the Destination analysis of *on the napkin*. Crucially, unambiguous forms that removed the conflict (e.g., *Put the frog that's on the napkin...*) posed no challenge for IG—his eye movements and actions were entirely normal. Together, these patterns suggest that IG developed an early Destination interpretation of the ambiguous phrase based on the verb *Put* and could not revise this commitment even after receiving conflicting linguistic evidence that signaled a new destination for the putting action (*into the box*). In the case of IG, this difficulty was connected to his impaired cognitive control, as indexed by his exaggerated PI effect.

Akin to the work reviewed above, research on comprehension deficits in aphasic patients has historically focused on sentence-level comprehension failures. There has also been, though, research investigating comprehension errors at the single-word level, which, in the spirit of the cognitive control hypothesis, has aimed to test the effects of competition during lexical comprehension. Lexical ambiguity resolution paradigms have been especially useful for examining such effects. In one study, a triplet lexical decision paradigm (Schvaneveldt and Meyer 1976) was administered to patients with LIFG damage (including IG) to examine whether this region plays a necessary role in context-dependent meaning selection (Bedny et al. 2007). In this task, the first word of the triplet serves as a cue, the second word is ambiguous (e.g., *bank*, which can refer to a financial institution or the side of a river), and the third word is the target. Reaction times are measured to the target. Two critical conditions were manipulated: in consistent conditions, the first and third words are related to the same meaning of the lexical ambiguity (e.g., *dollar – bank – money*); in inconsistent conditions, the first and third words are related to different—i.e., conflicting—meanings of the ambiguous word (e.g., *river – bank – money*). Compared to non-LIFG neuropsychological patients and healthy controls, a group of patients with a damaged LIFG did not make faster lexical decisions to target words in the consistent versus inconsistent condition, suggesting insufficient use of context for lexical ambiguity resolution. In a companion experiment, Bedny et al. demonstrated that, for patient IG in particular, LIFG damage did not completely eliminate priming: no differences emerged between consistent and inconsistent conditions, but IG was faster in the consistent condition relative to neutral trials, in which the first two words were unrelated to the target (e.g., *spoon – cloud – money*). In other words, ‘damage to the LIFG does not abolish contextual priming, but rather increases priming in the inconsistent condition. These findings suggest that damage to the LIFG interferes with the ability to suppress the context inappropriate meaning of ambiguous words, but does not affect the activation of context appropriate information’ (Bedny et al. 2007; p. 109).

Indeed, such findings are reminiscent of work by Swaab et al. (1997), who observed that selection of meaning context is significantly delayed in Broca’s aphasics: in an ERP experiment, these researchers demonstrated that while healthy adults rapidly resolve the context-appropriate meaning of an ambiguous word (within 100 ms), Broca’s aphasics do not show such rapid resolution (in fact, not until 1250 ms postpresentation). Taken together, what these lexical ambiguity studies show, in part, is a lack of an effect of the preceding context on word-meaning selection—in the work by Bedny et al., such a failure is clearly tied to LIFG damage (see Hindy et al. 2009; for recent evidence of the importance of LIFG in ambiguity resolution using transcranial magnetic stimulation in normal subjects). An inability to use semantic context to resolve lexical ambiguities naturally carries implications for sentence comprehension: it too will be deleteriously affected if one cannot seamlessly integrate words into a developing interpretation by discounting inappropriate meanings, as the sentence and context unfold incrementally (see also Hagoort 1989, 1993).

Conclusions and Unresolved Issues

In this article, we reviewed the evidence that has accrued since 2005 to support the hypothesis that the role of LIFG, including Broca’s area, in language processing is the same as the one it appears to play in general complex cognitive tasks: to regulate and control behavior in the face of competing representations. This is substantiated by findings in (i) the neuroimaging literature, which demonstrates within-individual co-localization

in LIFG for classic cognitive control tasks and sentence processing tasks that manipulate demands for control; (ii) the developmental literature, demonstrating young children's failure to countermand dominant interpretations despite other sources of evidence; in at least two studies, this was shown to depend on variations in cognitive control abilities; and (iii) the neuropsychological literature, which offers a host of results for LIFG patients: they exhibit inflated difficulty on general cognitive tasks when demands for control are manipulated to be high and by extension selective language production and comprehension difficulties that are tightly bound to this general cognitive control deficit.

However, there are of course other theories about the role that ventrolateral PFC, including LIFG, plays in cognition and cognitive control in particular. For example, one influential view contends that LIFG supports a top-down biasing signal that guides the controlled recovery of meaning from long-term memory, when semantic knowledge cannot be retrieved automatically (i.e., does not easily come to mind), regardless of competition- or conflict-related demands (Wagner et al. 2001). Notably, though, the effects observed in those studies (e.g., Badre and Wagner 2002) were observed in more anterior regions of ventrolateral PFC (BA 47; see Figure 1), not the posterior regions under discussion here (BA 44/45). Thus, research exists that investigates functional subdivisions within this region more broadly (cf. Badre and Wagner 2002; Badre et al. 2005; see also Donohue et al. 2005; Nagel et al. 2008). Martin et al. similarly assert that cognitive control is necessary when one has trouble recovering a response from memory, requiring effortful, attention-demanding retrieval (Martin and Cheng 2006). These hypotheses could theoretically account for some of the findings reviewed here (see Novick et al. 2009 for a discussion); thus future research should attempt to disentangle these perspectives (see also Hagoort 2005 for related discussions of subdividing frontal regions, instead based on levels of linguistic content).

Another alternative view on the function of Broca's area is that this region supports syntactic complexity (in particular, 'movement') during language processing (Ben-Shachar et al. 2003; for a comprehensive review, see Grodzinsky and Santi 2008). This account stems generally from the following findings: (i) this region is activated when healthy participants read passive versus active constructions while undergoing fMRI and (ii) Broca's aphasics have difficulty comprehending passive—i.e., more complex—constructions (though the authors do not make the important distinction between Broca's aphasics and patients with circumscribed damage to Broca's area). Although the syntactic complexity account is intriguing, the increased LIFG activation for the processing of complex constructions like passives (e.g., Ben-Shachar et al. 2003) may not reflect syntactic complexity per se, but instead the need to bias interpretation commitments away from the canonical active construction so that the activation levels can be regulated toward the less frequent, conflicting alternative (i.e., the passive construction; see January et al. 2009; Novick et al. 2005). Other researchers have also offered interpretations of sentence complexity effects that may be understood in such cognitive control terms; for instance, Van Dyke and Lewis (2003) ascribe individuals' difficulty revising misunderstood sentences to an interference-resolution process (Van Dyke and Lewis 2003).

Finally, there are additional results that suggest other putative functions of Broca's area, which may be difficult to explain under the cognitive control argument. For instance, posterior LIFG, particularly BA 44, is activated when participants listen to and rehearse polysyllabic pseudowords, suggesting auditory and motor involvement in speech processing (e.g., Buchsbaum et al. 2001). As well, temporarily disrupting Broca's area through transcranial magnetic stimulation results in speech arrest even during simple tasks like counting (Stewart et al. 2001). And BA 44 is also activated during both the observation

and imitation of finger movements, suggesting involvement in planning motor actions (Iacoboni et al. 1999). While these findings may appear to be inconsistent with the cognitive control theory on the surface, they may be explained by a finer-grain functional partitioning of Broca's area that parallels the region's anatomical subdivisions. Future research should test whether the anatomically distinct areas within LIFG (e.g., dorsal and ventral regions of BAs 44 and 45) map onto separate functions, for instance speech motor processes versus higher-level functions like cognitive control.

In closing, we assert that common cognitive control mechanisms underlie LIFG involvement in a range of tasks—a viewpoint that carries important implications for language processing. This account, alongside careful manipulation of demands for control and within-individual fMRI designs, has permitted thorough examination of exactly when LIFG engages across task types, thus shedding light on the critical commonalities between certain language processing conditions and the need for cognitive control. Such a framework has also enabled researchers to begin to characterize more precisely the nature of the language abilities (and disabilities) of patients with circumscribed damage here, and of young children whose PFC development is relatively long-drawn-out. Although Broca's area has traditionally been assigned the core function of sentence processing—including producing and comprehending intricate grammatical forms—it is clear that LIFG patients' cardinal failure does not involve processing difficult linguistic information *per se*. Indeed, in the right circumstance, such a patient is effortlessly able to say, with all its grammatical complexity, 'That one, every time you go by, it sings', but is decidedly unable to produce words in the presence of semantic distractors (see also Linebarger et al. 1983, for similar patients' sensitivity to grammatical structure). Likewise, LIFG patients fail to understand lexical and sentence-level ambiguities even when context should help. Taken together, the question is: Why? Certainly, Luria's early observation is apt: patients with anterior lesions have difficulty producing language in unconstrained contexts—but not necessarily in others—suggests that their failure may not be language specific. By unraveling the components of a range of linguistic tasks, and by carefully scrutinizing their general cognitive abilities, one sees that describing the language profile of patients with restricted Broca's area injury may be best understood in terms of their ability to regulate and control their linguistic behavior.

Short Biographies

Jared Novick is an Assistant Research Scientist at the University of Maryland in the Center for Advanced Study of Language and Department of Psychology. He received his B.A. in Brain and Cognitive Sciences from the University of Rochester in 1998 and his A.M. and PhD in Psychology from the University of Pennsylvania in 2005. After Penn, Novick spent 2 years as a postdoctoral associate at MIT studying neuroimaging methods. His research investigates how people process language in real time, using a combination of neuroscience and behavioral techniques. One such technique is the recording of readers' and listeners' eye movements to obtain a moment-by-moment measure of their incremental parsing decisions. Novick's work examines both healthy adults and patients with brain lesions to understand the architecture of the human language system, and the extent to which general cognitive abilities—such as the mental ability to regulate thoughts and behavior—contribute to language processing. In addition to research, Novick is actively involved in student training. He is a passionate advisor to both undergraduate honors students and graduate students in Maryland's Psychology Department and Neural and Cognitive Science program. Novick was elected to MIT's chapter of Sigma

Xi and was recently awarded the title of 'Researcher on the Rise' at the Center for Advanced Study of Language.

John Trueswell is a Professor of Psychology and Director of the Institute for Research in Cognitive Science at the University of Pennsylvania. He earned his B.A. in Cognitive Science from the University of Rochester in 1988 and his Ph.D. in Psychology from the University of Rochester in 1993. Trueswell's laboratory focuses on understanding how children develop the ability to process language in real time and how this ability interacts with the acquisition of language. Trueswell is known for pioneering eye tracking methods designed for the study of spoken language processing in young children. In addition to his research, Trueswell is actively involved in undergraduate and graduate training in cognitive science at the University of Pennsylvania. He was the co-creator of the Annual Undergraduate Workshop in Cognitive Science and Cognitive Neuroscience, which he continues to direct. He is also director of the NSF-IGERT graduate program in Language and Communication Sciences.

Sharon Thompson-Schill is the Class of 1965 Term Professor of Psychology and Neurology at the University of Pennsylvania. She received her B.A. in Psychology from Davidson College in 1991 and her PhD in Psychology from Stanford University in 1996. Thompson-Schill's laboratory uses a multi-methodological approach to study complex human cognition in both normal and impaired individuals, with a focus on relationships between cognitive processes, such as language and cognitive control, or perception and memory. Early in her career, Thompson-Schill received a Searle Scholars Award for new biomedical faculty, and she was awarded the Young Investigator Award from the Cognitive Neuroscience Society, in recognition of her work on cognitive control. She was elected to the Board of Directors of the Association for Psychological Science in 2007, and she received the James McKeen Cattell Fund Fellowship in 2008. In addition to her research accomplishments, Thompson-Schill is an enthusiastic teacher of psychology and neuroscience. She is the Director of Undergraduate Studies in her department, she founded and continues to direct the Honors Program in Psychology at Penn, and she is the author of Barron's study guide for the Psychology GRE Test. Thompson-Schill has won numerous local and national teaching awards, including the Women in Cognitive Science Mentorship Award and Penn's Lindback Award for Distinguished Teaching.

Note

* Correspondence address: Jared M. Novick, University of Maryland, Center for Advanced Study of Language, Box 25 College Park, MD 20742, USA. E-mail: jnovick1@umd.edu

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