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Investigations of the syntax-brain relationship

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Investigations of the syntax-brain relationship

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Cognitive Neuroscience

by

William Gerald Matchin

Dissertation Committee:
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2014

DEDICATION

To my family, friends, and mentors.

> “For to be possessed of a vigorous mind is not enough; the prime requisite is rightly to apply it. The greatest minds, as they are capable of the highest excellences, are open likewise to the greatest aberrations; and those who travel very slowly may yet make far greater progress, provided they keep always to the straight road, than those who, while they run, forsake it.”

René Descartes

Discourse on the Method

“It is the responsibility of intellectuals to speak the truth and to expose lies.”

Noam Chomsky

“The responsibility of intellectuals”

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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4. **Matchin, W**., Ferrill, M., Rogalsky, C., Love, T., & Hickok, G. (2011). Role of the motor system in audio-visual speech integration: evidence from the McGurk effect in Broca's aphasia. Poster presented at the 18th annual meeting of the Cognitive Neuroscience Society.

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ABSTRACT OF THE DISSERTATION

Investigations of the syntax-brain relationship

By

William Gerald Matchin

Doctor of Philosophy in Cognitive Neuroscience

University of California, Irvine, 2014

Professor Gregory S. Hickok, Chair

This dissertation critically examines extant hypotheses on the syntax-brain relationship, particularly proposals concerning Broca's area, and presents empirical data in efforts to localize syntactic operations in the brain. Chapter 2 of the dissertation reviews arguments for and against a role for Broca's area in syntax, and presents an fMRI experiment using a construction called *backward anaphora* in which the activity in the *pars triangularis* of Broca's area is shown to pattern with how sentences are processed (i.e., whether the construction involves *active* processing), and not their syntactic properties (i.e., activity is not contingent on *Movement* constructions). Chapter 3 extends Dehaene & Cohen's *neuronal recycling* hypothesis (Dehaene & Cohen, 2007) to language function in Broca's area to account for sentence-selective activations in this region of cortex (Fedorenko et al., 2012). In particular, the discussion in Chapter 3 focuses on language- or sentence-specific working memory (Caplan & Waters, 1999), and how language-specific working memory may develop out of domain-general working memory. Chapter 4 presents an fMRI experiment aimed at uncovering the neural basis of syntax using a "syntactic perturbation" technique during overt sentence production. In addition, the

experiment specifically examined the response profile of Broca's area and another region classically implicated in structural processing, the anterior temporal lobe (ATL), to our novel manipulation targeting syntactic structure. The results, when compared to perturbation in a control condition of unstructured word lists, revealed preferential activation for syntactic perturbation in networks previously implicated in motor control (Tourville et al., 2008) and action inhibition (Aron et al., 2014), including the basal ganglia, thalamus, and right inferior frontal gyrus, suggesting that (i) sentence production allows greater phonological/articulatory planning than list production, and (ii) syntax may rely on networks similar to basic motor control. However, effects at the syntax level are conflated with effects at lower motor levels in our experiment. Broca's area and the ATL did not exhibit effects consistent with syntactic processing, although our results extended the basic finding of increased activation to sentences compared to word lists previously found in the ATL (Mazoyer et al., 1993). Finally, Chapter 5 concludes the dissertation.

Chapter 1

Introduction

Efforts to understand the neural basis of language have been in progress since the 19th century, with the initial steps having been taken by the classical aphasiologists Broca, Wernicke, and Lichtheim, who schematized the neural localization of processes involved in speech perception and production (Poeppel & Hickok, 2004). Of course, a proper, modern definition of language would be quite empty without including the core, generative system governing the structure of sentences referred to as syntax; a component of language not seriously recognized and studied until the cognitive revolution of the 1950s and 60s and Noam Chomsky's revolutionary work on generative grammar (Chomsky 1957; 1965). Since the genesis of scientific investigation into the connection between language and brain, substantial progress has been made in elaborating the characterization of neural networks involved in the production and perception of speech (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009), with some additional forays into lexical-semantic processing (Lau et al., 2008; Binder et al., 2009) and domain-general functions such as cognitive control and working memory (Thompson-Schill et al., 1997; Badre & D'Esposito, 2007), among others. However, it seems to me that the field currently has no good ideas about the neural instantiation of syntax. This is a troublesome and somewhat embarrassing state of affairs for a neurolinguist to be in. To borrow a turn of phrase from Jerry Fodor: it is not hard to be mildly depressed at having nothing cogent to say about the connection between the brain and the core of language. With a bit of work, however, perhaps we can develop some more plausible hypotheses and work off the funk. This dissertation evaluates existing hypotheses about syntax and Broca's area, elucidates some of the issues involved in understanding the syntax-brain relationship, and attempts to provide new insight and direction to studying it. In doing so, I will present empirical data collected in my graduate career and theoretical discussion of these and extant data.

There are those that disagree with this grim assessment, of course. In particular, there are those that deny the existence or importance of syntax, hierarchical structure, and/or symbolic rules in language at all (Frank, Bod & Christiansen, 2012; Rumelhart & McClelland, 1985), or do not think of syntax as the central piece of the genetic endowment for language (Tomasello, 2009; Everett, 2012). For them, the lack of good hypotheses of the neural instantiation of syntactic operations is moot. This dissertation will not address these opinions, leaving the matter to competent individuals in the relevant domains.

Other researchers share the perspective that syntax is an essential and central component of language, but posit instead that we have *good* ideas about the neural localization of syntax: namely, Broca's area, or parts thereof (Grodzinsky & Santi, 2008; Friederici et al., 2011; Hagoort, 2005). This dissertation follows the tradition of the Hickok lab (Hickok, 2000; Rogalsky & Hickok, 2011) in rejecting these proposals as conflating syntactic operations with various nonsyntactic processes involved in language performance. Processing considerations are of extreme importance when investigating language, as well as any cognitive domain – such considerations were of paramount importance in Chomsky's separation of competence and performance (Chomsky, 1965). It has been observed for a long time that integrating syntactic theory into a model of actual language use is an extremely difficult prospect, as many factors outside of the core grammatical competence must be accounted for (Miller & Chomsky, 1963). Of course, this is exactly the task we are faced with when sticking subjects in the fMRI scanner and having them comprehend or produce sentences – this is actual language behavior, embedded in a galaxy of cognition, and our goal is to extract from that mess something to do with syntax.

This seems to be the problem with current proposals of syntactic operations in Broca's area – there are quite salient ramifications of non-syntactic processing mechanisms in Broca's area, rendering the syntax accounts suspect.

Where do we go from here? It may very well turn out that the important discoveries will only come when we understand more about how neurons actually store and process information (Gallistel & King, 2008). At the very least, considering more seriously what David Poeppel called the "mapping problem" (Poeppel, 2012) will be crucial to moving things forward, as well as more carefully considering the nature of on-line processing and incorporating processing considerations into neuroimaging studies. The final chapters of this dissertation approach the localization of syntax from this perspective.

The dissertation begins in Chapter 2 by expanding on the issues surrounding Broca's area and syntax, including experimental data in fMRI that demonstrate that activations to long-distance dependencies are contingent on how they are processed, not their syntactic construction, advocating a domain-general account of this region's function, rather than one of syntactic operations. In particular, it assesses the claim that the transformational operation "Movement", a core component of generative syntax (Chomsky, 1982), is processed by Broca's area (Grodzinsky, 2000; Grodzinsky & Santi, 2008). The critical manipulation in our study was a distance manipulation in backward anaphora, a non-Movement long-distance dependency between an anaphor (i.e., pronoun) and its antecedent, that resulted in activation in the anterior portion of Broca's area, indicating a domain-general function rather than one tied to Movement.

It continues in Chapter 3 by resolving concerns about the function of Broca's area in light of activations there that are sentence-specific, not reducible to domain-general working memory or cognitive control, by positing the neuronal retuning of these domain-general functions throughout an organism's development for language-specific inputs. Chapter 4 comprises the final part of the dissertation: an fMRI experiment aimed at uncovering the neural instantiation of syntax with a novel approach to this issue, using a 'syntactic target perturbation' technique, and Chapter 5 concludes.

Chapter 2

On the relation between Broca's area and syntax: a distance effect for backward anaphora in the anterior portion of Broca's area

Language can be characterized as a cognitive faculty consisting of several components, including a core recursive and generative structure-building system referred to as syntax (Chomsky 1981; 1995; Hauser et al., 2002). Syntax consists of basic structure-building mechanism(s) that generate hierarchical phrase structure (e.g., *Merge*), transformational operations that modify phrase structure (e.g., *Move*), and various additional properties and grammatical constraints. Of concern in this dissertation are basic structure-building and transformational operations. Syntax is of particular interest in language because it governs the capacity for the unbounded generation of sentences, defines the relationships among lexical elements for semantic interpretation, and forms the basis of phonological structures for perception and production (Chomsky, 1982). As such, there has been much research into the neural basis of syntactic operations as a core part of the language faculty. Much work on syntax and sentence processing has focused on Broca's area, the left inferior frontal gyrus (LIFG; Brodmann areas 44 and 45), but hypotheses concerning Broca's area, syntax, and sentence comprehension remain controversial, with some authors arguing that subregions within Broca's area underlie specific syntactic operations (Grodzinsky & Friederici, 2006; Hagoort, 2005; Grodzinsky, 2008; Friederici et al., 2011) and others arguing for a role contingent on domain-general processing, such as working memory or cognitive control (Stowe et al., 2005; Kaan & Swaab, 2002; Rogalsky & Hickok, 2011; Bornkessel-Schlesewsky & Schlesewsky, 2013; Novick et al., 2005). This chapter of the dissertation focuses on resolving the debate around the involvement of the LIFG in syntax.

Other candidates in the literature of the neural basis for syntax include the anterior temporal lobe, or ATL (Mazoyer et al., 1993; Humphries et al., 2005; Rogalsky & Hickok, 2009; Brennan et al., 2012; Bemis & Pylkkanen, 2011), and subcortical structures, particularly the basal ganglia (Ullman et al., 1997; Pinker & Ullman, 2002; Ullman, 2004; Lieberman, 2009). While investigation into the relationship of the ATL and syntax continues, there appears to be fairly strong evidence that patients with damage confined to the ATL do not show deficits in syntax (Mesulam, 2013; Wilson et al., 2014), while these patients have striking deficits in semantics (Hodges et al., 1992). I will not discuss the ATL additionally in this chapter, besides noting that it does activate consistently more for sentences than to lists of words, suggesting some role in sentence comprehension, and is likely an important component of the network involved in language – probably semantic processing of some kind (Lau et al., 2008; Bemis & Pylkkanen, 2011), but see Chapter 4 for more extensive discussion of the neuroimaging literature. The basal ganglia are certainly an interesting possibility for the localization of syntactic operations, among other subcortical structures such as the thalamus and cerebellum. Such proposals have garnered relatively little attention compared to Broca's area and the ATL, but may turn out to play a key role. I will postpone speculation on this front until Chapter 4, and focus here on the role of Broca's area in sentence processing, concluding against a role for it in syntactic operations, although involved in sentence processing through domain-general contributions.

2.1 Introduction

It is a relatively undisputed that Broca's area shows increased response in functional magnetic resonance imaging (fMRI) to sentences with noncanonical word order (Stromswold et al., 1996; Friederici et al., 2006b; Makuuchi et al., 2009; Santi & Grodzinsky, 2007a; Bornkessel et al., 2005; Rogalsky et al., 2008). However, activations to such manipulations do not clearly establish a role for some subregion(s) of Broca's area in syntactic operations. Distinguishing among syntax-specific or domain-general alternatives is difficult because sentence contrasts based on structure are often conflated with one or more processing differences. The goal of the experiment reported in this chapter was to better tease apart the contribution of syntactic and processing factors to activation in Broca's area using a novel construction known as backward anaphora (or perhaps more succinctly, cataphora). This work was carried out in collaboration with my thesis advisor, Gregory Hickok, and my co-advisor, Jon Sprouse.

The current experiment builds on previous studies that manipulated distance between a displaced wh-word and gap location in filler-gap constructions (Fiebach et al., 2005; Santi & Grodzinsky, 2007a; Santi & Grodzinsky, 2010), and one study comparing distance effects in filler-gap constructions to manipulations of the distance between an antecedent and a pronoun in canonical anaphoric dependencies (Santi & Grodzinsky, 2007a). This study revealed activation in an anterior portion of Broca's area in the vicinity of Brodmann area 45 (BA45) in the pars triangularis for filler-gap dependencies but not for canonical anaphoric dependencies. Because filler-gap dependencies involve syntactic movement while canonical anaphoric dependencies do not, these results have been interpreted as evidence for a syntactic account of Broca's area (Santi & Grodzinsky, 2007a). However, filler-gap dependencies and canonical anaphoric dependencies also differ along an important dimension of sentence processing that could have been responsible for the difference in activation: filler-gap dependencies trigger an active prediction mechanism that attempts to complete the dependency as incoming material is parsed (Crain & Fodor, 1985; Stowe, 1986; Frazier & Flores d'Arcais, 1989), while canonical anaphoric dependencies do not trigger such a prediction mechanism and instead involve a mechanism that searches backward through the memory encoding of previously parsed material for the antecedent of the pronoun. Backward anaphoric dependencies eliminate this confound by reversing the order of the antecedent and pronoun such that the pronoun precedes its "antecedent". Backward anaphoric dependencies have been shown to engage an active prediction mechanism similar to the one engaged by filler-gap dependencies (Kazanina et al., 2007a; van Gompel & Liversedge, 2003). In this way, a comparison between filler-gap dependencies and backward anaphoric dependencies better isolates the syntactic difference between filler-gap and anaphoric dependencies (movement versus no-movement) while controlling for processing differences (both involve active prediction mechanisms).

The experiment reported in this chapter reveals a syntactic distance effect for backward anaphora in the *pars triangularis* of Broca's area. These results suggest that this region is not selectively sensitive to the syntactic operation underlying filler-gap dependencies (e.g., wh-movement), but instead is sensitive to the processing of long-distance dependencies that involve active prediction mechanisms. The results reported here do not isolate exactly which aspects of the prediction mechanisms are responsible for the observed activity (e.g., syntactic working memory mechanisms, cognitive control, or syntax-specific aspects of the prediction such as the application of abstract structural constraints on the locations of gaps and antecedents), but they do serve to further narrow the space of possible roles for the *pars triangularis* of Broca's area in sentence comprehension.

2.1.1 Long-distance dependencies and Broca's area

Long-distance dependencies are relationships between non-adjacent elements in a sentence. One type of long-distance dependency is filler-gap dependencies: so-called because they consist of an element (the filler) that appears to be displaced from a position (the gap) later in the sentence. Sentence (1) demonstrates one example of a filler-gap dependency, a WH-question. Subscripts indicate the relationship between the filler and the gap:

(1) [Which cat]$_1$ did the dog chase ___$_1$?

In order to derive the correct meaning of (1), *which cat* must be interpreted at the gap location as the object of the verb *chase*. Filler-gap dependencies are analyzed in generative syntax as an instance of syntactic Movement (e.g., Chomsky, 1982; Chomsky, 1995). Movement is an operation whereby an element at some position in the sentence is displaced to a position that is both higher in the structure and earlier in the linear order of the sentence. Movement results in filler-gap dependencies, as the moved element must be linked to its base-generated position for successful interpretation of the sentence. Brain imaging studies have consistently demonstrated an association between Broca's area and distance manipulations in syntactic movement (Fiebach et al., 2005; Friederici et al., 2006b; Santi & Grodzinsky, 2007a; Santi & Grodzinsky, 2010). For example, Santi & Grodzinsky (2007a) parametrically increased the distance between a moved noun phrase (NP) and its gap by inserting intervening NPs, showing that an anterior portion of the *pars triangularis* (BA45) exhibits a linear increase in activity with distance. These imaging results converge with previous evidence in patients with Broca's aphasia, who appear to have a comprehension deficit selective to sentences with movement (Grodzinsky, 2000). To account for this deficit, Grodzinsky (2000) developed the Trace-Deletion Hypothesis (TDH), according to which the agrammatic deficit in Broca's aphasia consists of an inability to compute filler-gap dependencies due to damage in Broca's area. The hypothesis stemming from the combined results of lesion and neuroimaging studies is the syntactic movement hypothesis of Broca's area (Grodzinsky, 2008), which holds that the region is responsible for the computation of syntactic Movement during comprehension. The data supporting an association between Movement and Broca's area are broadly consistent with other accounts of the region's role in sentence processing, such as the accounts proposed by Friederici and colleagues, which posit that various subregions of Broca's area support hierarchical syntactic processes (Bahlmann et al., 2008; Friederici 2011; Friederici et al., 2006a; 2006b; Grodzinsky & Friederici, 2006) or 'syntactic working memory' (Fiebach et al., 2005), and the accounts proposed by Hagoort and colleagues, which posit that Broca's area supports syntactic and semantic unification during sentence processing (Hagoort 2005; Snijders et al., 2009).

2.1.2 Activations in Broca's area during sentence processing: syntactic operations or domain-general processing?

The Movement hypothesis and related claims share the fundamental assertion that Broca's area supports a specific syntactic operation. Alternatively, some hypotheses posit that activation in Broca's area during sentence comprehension reflects domain-general processes. For instance, Kaan & Swaab (2002) reviewed several neuroimaging studies of syntactic processing and concluded that Broca's area likely contributes to sentence comprehension by contributing additional resources when processing load increases. This conclusion is consistent with the verbal working memory account proposed by Rogalsky, Hickok and colleagues (Rogalsky et al., 2008; Rogalsky & Hickok, 2011), which posits that the posterior portion of Broca's area in the *pars opercularis* contributes to the comprehension of complex sentences via its role as the articulatory component of a phonological loop in working memory (Baddeley & Hitch, 1974; Baddeley, 1981). This claim is supported by Rogalsky et al. (2008), who showed that articulatory suppression interfered with comprehension of more complex sentences to a greater extent than comprehension of simpler sentences in healthy young adults (fig. 2.1). In addition, the fMRI portion of this study showed that additional activation in the *pars opercularis* due to a sentence complexity manipulation (fig. 2.2, top) was eliminated under conditions of articulatory suppression (fig. 2.2, bottom left). Rogalsky et al. interpret this as evidence that verbal working memory resources were saturated by articulatory suppression and unavailable during sentence comprehension. Despite this potential verbal working memory explanation for activation in the *pars opercularis*, Rogalsky et al. did not find that articulatory rehearsal could account for activations in the anterior portion of Broca's area in the *pars triangularis* (fig. 2.2, bottom right), so it remains possible that this region could support syntax-specific processes.

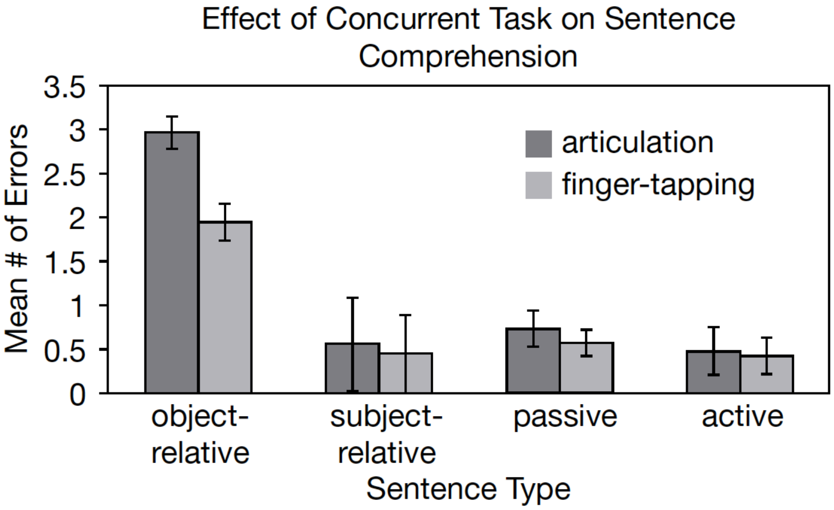


Figure 2.1 (adapted from Rogalsky et al., 2008). A simultaneous articulatory rehearsal task impaired comprehension of complex object-relative sentences (e.g., *the man that the boy pushed is wearing a red shirt*) relative to a finger-tapping control task, while simpler sentence constructions showed no such effect.

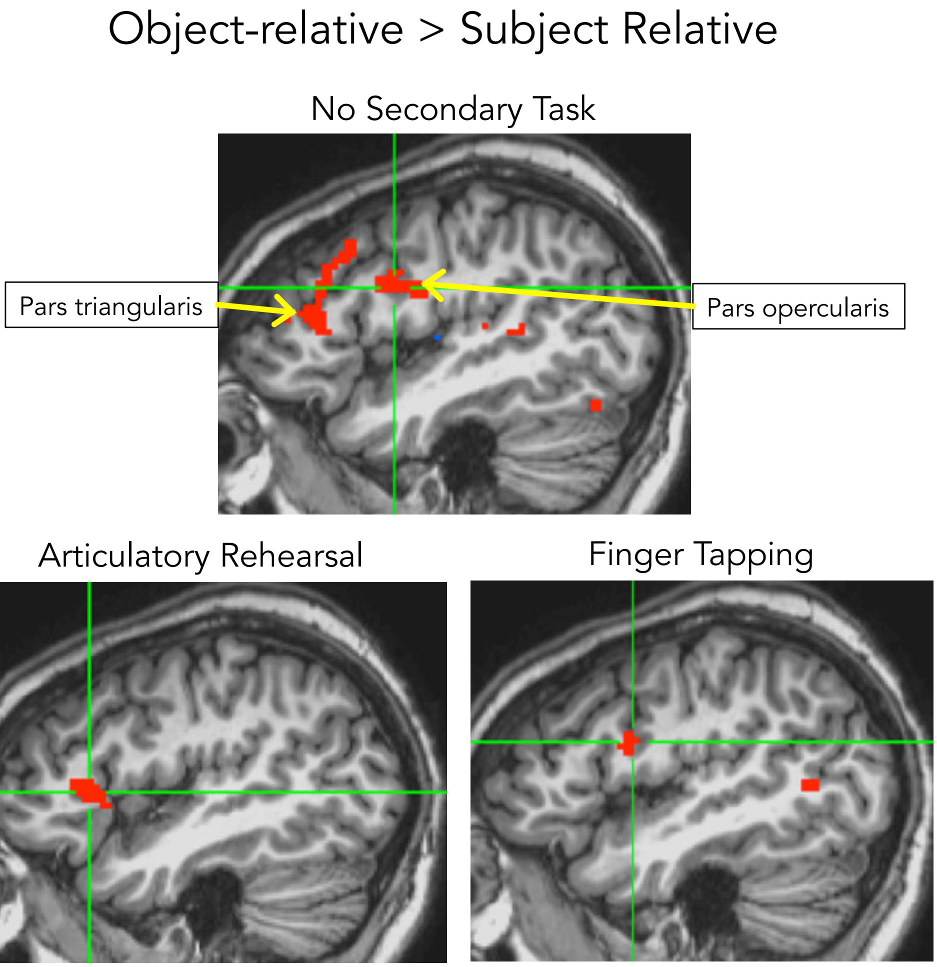


Figure 2.2 (adapted from Rogalsky et al., 2008). Activations for sentence complexity, object-relative > subject relative. TOP: activation for complexity without any secondary task. BOTTOM LEFT: activation for complexity with concurrent articulatory rehearsal; activation in *pars opercularis* disappears. BOTTOM RIGHT: activation for complexity with concurrent finger-tapping; activation in *pars triangularis* disappears.

Another domain-general processing account of Broca's area's role in language is the cognitive control (Novick et al., 2005; 2010) hypothesis, which posits that increased activation during sentence processing results from competing representations that must be ruled out and suppressed. This account is supported by data from January et al. (2009), who showed co-localized activation in Broca's area for a stroop task and a sentence comprehension task involving syntactic ambiguity, suggesting that the region supports a domain-general cognitive control mechanism.

In addition to syntactic operations and domain-general processing, a third possibility is that activations in Broca's area reflect sentence-specific mechanisms during comprehension and/or production not comprising a purely syntactic operation. For instance, Bornkessel-Schlesewsky, Schlesewsky and colleagues have found that the *pars opercularis* of Broca's area shows increased activation with increased difficulty in argument linearization, that is, in assigning thematic roles (e.g., agent, patient) to the participants in a sentence (Bornkessel et al., 2005; Bornkessel-Schlesewsky et al., 2009). Dissociating among these accounts remains a difficult task for clarification of the roles of the different subregions of Broca's area during sentence processing. For a more elaborate discussion of the evidence in favor of domain-general accounts of Broca's area function in sentence processing, see Rogalsky & Hickok (2011).

The question of functional specificity in this brain region remains under contention, although evidence has been offered to distinguish among the alternatives. In the study by Santi & Grodzinsky (2007a), the distance effect found for the movement condition did not hold for another type of long-distance dependency, anaphora. An anaphoric dependency is the co-reference between an anaphor (a pronoun or reflexive) and the noun to which it refers (the antecedent). Sentence (2) illustrates such a dependency:

(2) [The boy]$_1$ fell down the stairs and hurt himself$_1$.

Movement and binding constructions are similar in that they both involve a long-distance (non-adjacent) dependency. Because of this, they presumably share some general cognitive demands, such as the working memory required to retrieve the filler/antecedent and integrate it into the context. Despite this similarity, Santi & Grodzinsky (2007a) found that distance in filler-gap dependencies modulated activity in Broca's area, but distance in anaphoric dependencies did not. This suggests selectivity in the response of this region to the syntactic difference between the two conditions, namely syntactic movement, rather than the domain-general similarities.

However, there is at least one important processing difference between the movement and binding conditions in Santi & Grodzinsky (2007a). In sentences with filler-gap dependencies, the filler always precedes the gap, and serves as a cue to the existence of the long-distance dependency. There is substantial evidence in the sentence processing literature that the parser uses the filler as a cue to engage a prediction mechanism that actively posits a gap location at the first grammatically licensed location that it encounters while parsing the incoming material. This prediction mechanism has been shown to be "active" in the sense that the parser does not appear to wait for unambiguous evidence for the gap location, and can therefore be shown to incorrectly posit gap locations at potential, but not actual, gap locations (Crain & Fodor, 1985; Stowe, 1986; Frazier & Flores d'Arcais, 1989, Garnsey et al. 1989, Traxler and Pickering 1996). In contrast, the linear order of antecedent and pronoun in anaphoric dependencies prevents the possibility of a prediction mechanism. Instead, the pronoun indicates the existence of an anaphoric dependency, and the parser engages in a backward search through memory for the previously encountered antecedent. In this way, the movement sentences in the Santi and Grodzinsky (2007a) experiment involved both syntactic movement AND an *active prediction* mechanism, while the binding sentences involved no movement and no prediction mechanism. It is possible that this active prediction mechanism may account for the asymmetric activity found in Broca's area.

2.1.3 Backward anaphora & the present experiment

The current experiment sought to tease apart the contribution of syntactic movement and the active prediction mechanism to activity in Broca's area during the processing of long-distance dependencies. To do this we, contrasted filler-gap dependencies with *backward anaphora*. Crucially, in backward anaphora the pronoun *precedes* the antecedent leading to a configuration in which the pronoun/reflexive can act as a reliable cue to invoke an active prediction mechanism for the antecedent:

(3) Because he$_1$ fell down the stairs, the boy$_1$ went to the hospital.

van Gompel & Liversedge (2003) found that subjects actively predict a coreferential relationship between potential antecedents to the pronoun in these constructions. They presented subjects with sentences like (4a) and (4b):

(4a) When he$_1$ was fed up, the boy$_1$ visited the girl very often.
(4b) When she$_1$ was fed up, the **boy** visited the girl$_1$ very often.

In (4a), the first noun phrase matches the gender of the first NP; in (4b), it does not. Subjects showed slower reading times to the first NP in (4b) relative to (4a), suggesting that the parser predicted a coreferential relationship with the NP in the subject position of the matrix clause before determining the gender of the noun, and had to reanalyze this relationship after the gender was determined. Using backward anaphora, it is possible to tease apart the contribution of syntactic movement and these prediction mechanisms to activation in Broca's area. To do so, we used a 2x2 design, with factors DISTANCE (short, long) and CONSTRUCTION (filler-gap, backward anaphora). In addition, we added an articulatory rehearsal condition to determine areas involved in speech production in order to account for effects due to verbal working memory. We found a significant main effect of distance in the *pars triangularis*, with no significant interaction between distance and construction in this region. However, upon investigating effects of distance within each construction separately, we only observed an effect of distance for the backward anaphora condition in the *pars triangularis*, while failing to replicate previously established distance effects in the filler-gap condition (Movement) in the this region (see section 4.2 for a discussion). The results suggest that it is unlikely that Broca's area subserves a specific syntactic process, although it is possible that it supports either sentence-specific or domain-general processing mechanisms depending on which aspect of the active prediction mechanisms are driving the activation (see section 4 for discussion).

2.2 Materials and methods

2.2.1 Subjects

Twenty-six right-handed, native speakers of English (age 19-32, 12 males) volunteered for participation. Subjects had normal or corrected-to-normal vision, no hearing impairment, and reported no history of neurological disorder. Subjects were paid $30 an hour for participation. Consent was acquired from each subject before participation and all procedures were approved by the Institutional Review Board of UC Irvine.

2.2.2 Stimuli and Design

Stimuli were auditory recordings of sentences from a male native English speaker. Filler-gap sentences (WH) consisted of WH-questions in which a matrix clause was modified by an adjunct clause, and the WH-question was formed by displacement of the matrix clause object to the front of the sentence (5a). Backward anaphora sentences (BA) consisted of a fronted causal adjunct clause containing a pronoun (e.g., *Because he/she did something…*), followed by a brief pause, and the matrix clause with an antecedent for the pronoun in the subject (6a). One hundred matched pairs of sentences (short/long) were created for both constructions. Distance for both dependency types was manipulated with a relative clause: short sentences contained a relative clause at the end of the sentence (5a, 6a); long WH sentences contained a relative clause modifying the subject of the matrix clause (5b); and long BA sentences contained a relative clause modifying the object of the fronted causal adjunct clause (6b):

(5a) WH-SHORT: Which song$_1$ did the band play __$_1$ at the concert **[that ended early]***?*

(5b) WH-LONG: Which song$_1$ did the band **[that won the contest]** play __$_1$ at the concert?

(6a) BA-SHORT: Because he$_1$ extinguished the flames, the fireman$_1$ saved the resident **[that arrived later]**.

(6b) BA-LONG: Because he$_1$ extinguished the flames **[that burned all night long]**, the fireman$_1$ saved the resident.

Pairs of sentences within each construction were matched for approximate content and number of syllables. Duration of sentences for each condition: WH-SHORT (mean=4.24s, standard deviation =0.40s), WH-LONG (mean=4.24s, standard deviation=0.38s), BA-SHORT (mean=4.37s, standard deviation =0.5s), BA-LONG (mean=4.44s, standard deviation =0.51s). The complete set of materials can be found in the Appendix. In order to avoid familiarity effects, the matched pairs within each construction were divided into two lists, with each list containing fifty sentences from each construction, such that subjects never saw both members of a matched pair. Semantically anomalous sentences (ANOM) were created by generating WH and backward anaphora sentences in the same manner described above, and replacing a noun phrase with one that did not fit context due to animacy violations or selection restrictions (e.g., *Which bird did the orchestra that dazzled the audience play expertly and loudly during the musical? Because he vetoed the bill, the plant angered the congress that crafted the legislation*). Forty anomalous sentences were generated, distributed nearly equally across both constructions and distances (17 WH, 23 BA). All subjects saw the same set of forty anomalous sentences. Each subject was presented with 50 trials from each of the four conditions, and 40 anomalous trials, for a total of 240 sentence trials. In addition, subjects were asked to subvocally perform articulatory rehearsal of the sequence /pa-ta-ka/ for 50 trials (ART) in order to localize a verbal working memory network, for a combined total of 290 trials.

2.2.3 Procedure

Subjects were informed that they would be listening to sentences and deciding whether they “made sense” or not. Subjects were instructed to pay close attention to the sentences, understand the meaning of the sentence, and only press a button if they heard an anomalous sentence. During each run, a fixation cross was displayed on a screen. Subjects responded using a button box in the left hand (in order to minimize activations in the left hemisphere) after the offset of the sentence and before the next trial. During ART trials, the fixation cross would flicker red-blue-green at a rate of 2 Hz for 5s, which cued the subjects to articulate the sequence /pa-ta-ka/ without producing sound or opening their mouth while still making movements internal to the vocal tract including tongue movements. Auditory stimuli were delivered with Matlab software (Mathworks, Inc., USA), the Cogent toolbox (http://vislab.ucl.ac.uk/cogent_2000.php), and MR compatible insert headphones. Subjects were given ear covers to attenuate scanner noise. The experiment consisted of twelve runs – one practice run, 10 experimental runs, and one high-resolution anatomical scan. The practice run was intended to familiarize subjects with the task and stimuli. Within experimental runs, five trials of each of the four main conditions, five articulation trials, and four anomalous trials were presented to the subject in random order. The order of trials from each condition was randomized across runs. Each trial lasted a total duration of 10s, with the stimulus jittered from the onset at delays of 0s, 0.5s, 1s, and 1.5s to better capture the peak of the hemodynamic response. Due to a coding error, two subjects did not receive any articulation trials. These subjects were included in the primary analysis, but not the ART analysis. Due to a different coding error, one subject was presented with two identical runs. We considered the impact of repetition effects in this case to be relatively minor (a separate analysis with this subject excluded did not qualitatively change the results), therefore this subject was included in all analyses. The high-resolution anatomical image was collected last. The scanning session lasted about one hour in total.

2.2.4 fMRI Data Collection and Preprocessing

MR images were obtained in a Philips Achieva 3T (Philips Medical Systems, Andover, MA) fitted with an eight-channel RF receiver head coil at the high field scanning facility at UC Irvine. We first collected a total of 1530 T2*-weighted EPI volumes over 10 runs using Fast Echo EPI in ascending order (TR=2s, TE=25ms, flip angle = 90◦, in-plane resolution = 1.95mm × 1.95mm, slice thickness = 3mm with 0.5mm gap). The first four volumes of each run were collected before stimulus presentation and discarded to control for T1 saturation effects. After the functional scans, a high-resolution T1-weighted anatomical image was acquired in the axial plane (TR=8ms, TE=3.7ms, flip angle=8◦, size=1mm isotropic).

Slice-timing correction, motion correction, and spatial smoothing were performed using AFNI software (http://afni.nimh.nih.gov/afni). Motion correction was achieved by using a 6-parameter rigid-body transformation, with each functional volume in a run first aligned to a single volume in that run. Functional volumes were aligned to the anatomical image, and subsequently aligned to Talairach space (Talairach and Tournoux, 1988). Functional images were resampled to 2.5mm isotropic voxels, and spatially smoothed using a Gaussian kernel of 6mm FWHM.

First-level analyses were performed on each individual subject's data using AFNI's 3dDeconvolve function. The regression analysis was performed to find parameter estimates that best explained variability in the data. Each predictor variable representing the time course of stimulus presentation was entered into a deconvolution analysis that estimated parameters best representing the timecourse of the hemodynamic response function in percent signal change values. The following six regressors of interest were used in the experimental analysis: WH-SHORT, WH-LONG, BA-SHORT, BA-LONG, ANOM, and ART. The six motion parameters were included as regressors of no interest. A second-level analysis was then performed by summing the parameter estimates across each timepoint on the estimated timecourse for each condition for each subject, and entering these values from each subject and condition into AFNI's 3dANOVA2 function. A cluster-corrected threshold of $p < 0.05$ (FWE) was used to locate activity for the following contrasts ('>' indicates one-tailed tests, '-' indicates two-tailed tests): main effect of distance [LONG > SHORT], main effect of construction [BA - WH], interaction of distance and construction, and the simple effects of BA-distance [BA-LONG > BA-SHORT] and WH-distance [WH-LONG > WH-SHORT]. In order to examine whether distance effects were due to verbal working memory, we ran a separate analysis only including data from the 23 subjects who performed the articulation task, and added the following contrast: [[LONG > SHORT] > ART], in which the activation to articulatory rehearsal was subtracted from the main effect of distance.

2.3 Results

2.3.1 Behavioral

Responses to anomalous (ANOM) sentences were categorized according to signal detection theory (hits, misses, false alarms, and correct rejections), such that button presses to anomalous sentences were considered hits, and button presses to non-anomalous (WH and BA) sentences were considered false alarms. One subject was excluded from further analysis due to particularly poor discriminability (*d'* = 0.88). The remaining twenty-five subjects had a mean *d'* of 2.8 with a standard deviation of .7, indicating successful discriminability of anomalous sentences from normal sentences (by convention, d'=1.0 is considered threshold for discrimination). These subjects correctly identified anomalous sentences with a rate of 74% (standard deviation 18%), and correctly accepted normal sentences (WH and BA) with a rate of 97%, (standard deviation 3%). These results indicate that the remaining 25 subjects processed the meaning of the sentences during scanning, and importantly, did not identify normal sentences as anomalous with any frequency.

2.3.2 fMRI

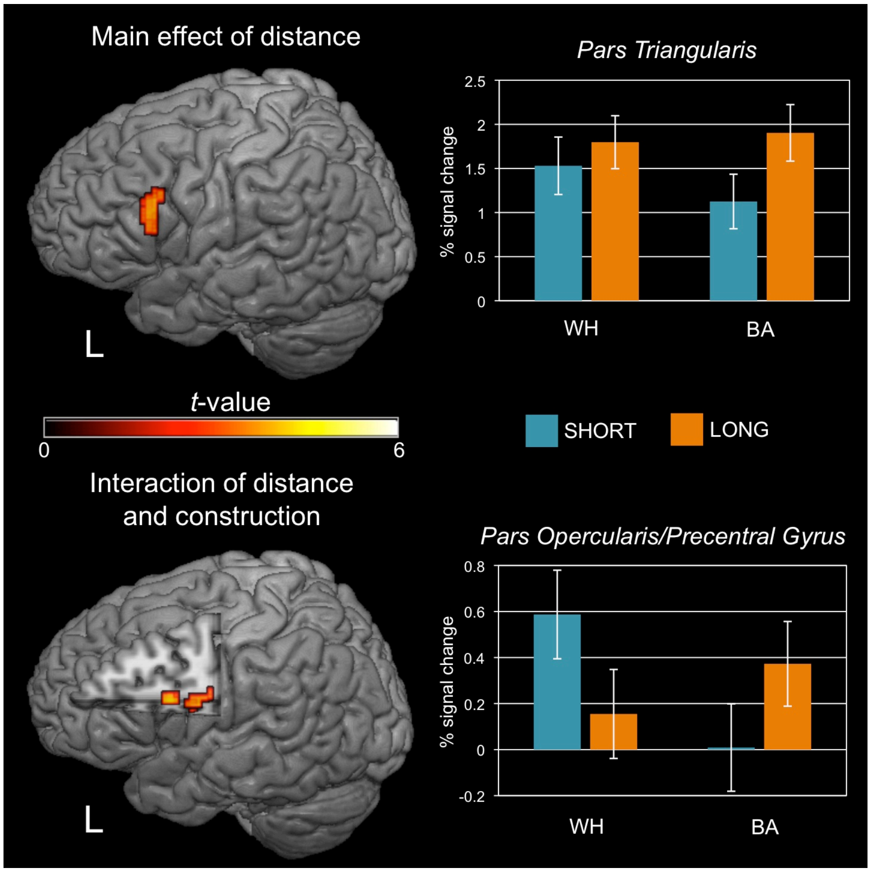


Figure 2.3. Group activation maps (*n* = 25) displayed in Talairach space on a template brain for the main effect of distance (top) and the interaction of distance and construction (bottom). Activations for the main effect of distance

were corrected for multiple comparisons (FWE) at $p < 0.05$ using an individual t-threshold of $p < 0.001$ (one-tailed) and a cluster size threshold of 608 mm^3. Activations for the interaction are displayed at a reduced cluster size threshold of 200 mm^3. Barplots indicate average percent signal change for each condition within selected clusters of activation (error bars indicate standard error of the mean).

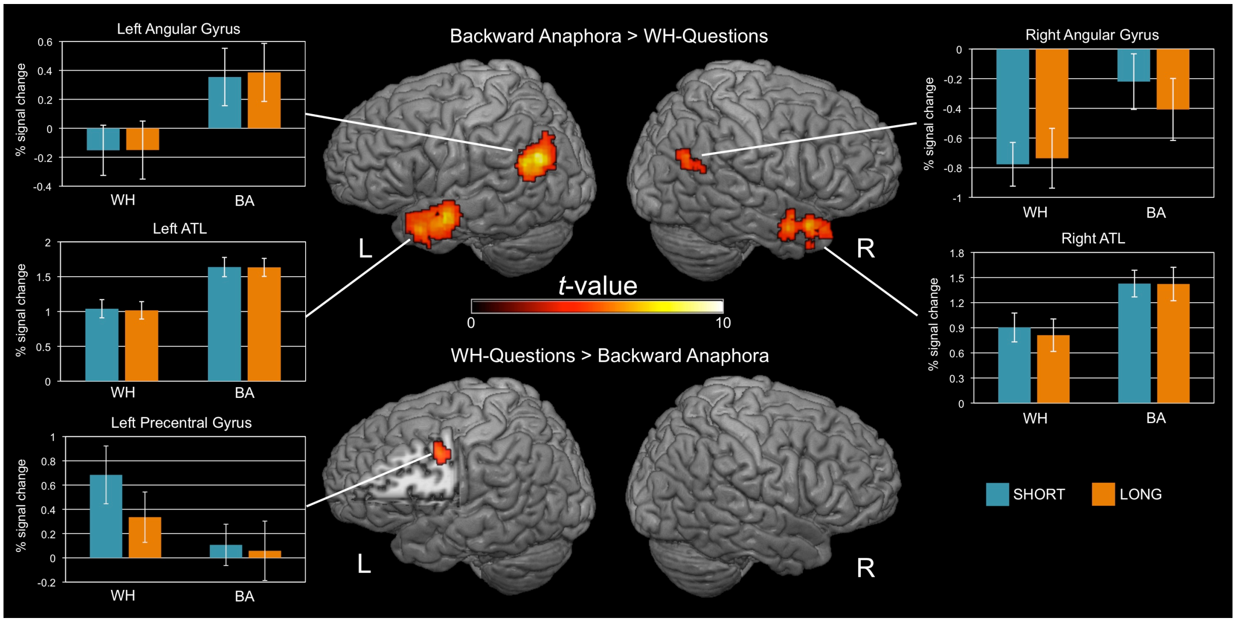


Figure 2.4. Group activation maps (n = 25) displayed in Talairach space on a template brain for the main effect of construction. Increased activation for Backward Anaphora sentences is shown on top, and increased activation for WH-questions is shown on bottom. Activations were corrected for multiple comparisons (FWE) at $p < 0.05$ using an individual t-threshold of $p < 0.001$ (two-tailed) and a cluster size threshold of 608 mm^3. Barplots indicate average percent signal change for each condition within selected clusters of activation (error bars indicate standard error of the mean).

The main effect of distance revealed one significant cluster of activity in the *pars triangularis* of Broca's area (left hemisphere; fig. 2.1, left). The interaction between distance and construction revealed no activity in this area. At a reduced cluster size threshold, there was a significant interaction in the left *pars opercularis* and left precentral gyrus, with increased activation for the BA-distance effect in this area (fig. 2.1, right). The main effect of construction, [BA > WH], revealed activity in bilateral ATL, bilateral angular gyrus, and bilateral precuneus/posterior cingulate (fig. 2.2, top), while [WH > BA] revealed activity in left precentral gyrus (fig. 2.2, bottom). As is noted in the discussion, the effect of distance was tightly controlled while the effect of construction was not (namely, the BA sentences consisted of three clauses, one of which was a fronted causal adjunct, while the WH sentences consisted of two clauses, with no causal adjunct), so any interpretation of the main effect of construction will be highly speculative.

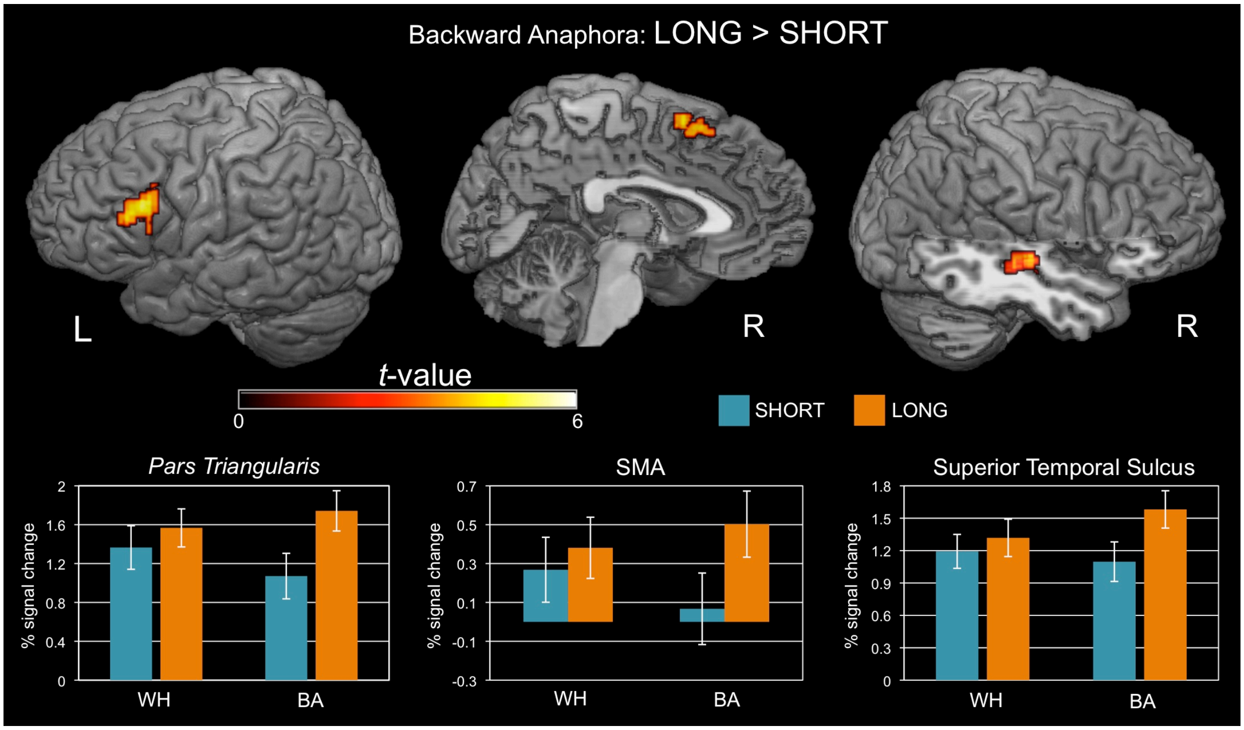


Figure 2.5. Group activation maps ($n = 25$) displayed in Talairach space on a template brain for the simple effect of distance in the Backward Anaphora condition. Activations were corrected for multiple comparisons (FWE) at $p < 0.05$ using an individual t-threshold of $p < 0.001$ (one-tailed) and a cluster size threshold of 608 mm^3. Barplots indicate average percent signal change for each condition within selected clusters of activation (error bars indicate standard error of the mean).

Although the interaction of distance and construction was not significant in the *pars triangularis*, we planned, *a priori*, to examine the simple effects of distance separately for each construction, as it is theoretically vital to establish a distance effect in the BA condition on its own. The simple effect of BA-distance [BA-LONG > BA-SHORT] revealed three clusters: one in the left IFG, *pars triangularis* (fig. 2.3, left), one in right middle temporal gyrus/superior temporal sulcus (fig. 2.3, right), and one in the supplementary motor area (bilateral; fig. 2.3, center). This result confirms our prediction that the novel backward anaphora condition would show a distance effect in the *pars triangularis* of Broca's area, given the active prediction mechanism employed in its processing. The simple effect of WH-distance ([WH-LONG-WH-SHORT]) did not reveal any significant activity. While this fails to replicate previous research documenting distance effects for movement constructions in Broca's area, it is not inconsistent with the observation that distance effects in this region may not be robust. For example, Santi & Grodzinsky found a cluster in the *pars triangularis* for the linear effect of distance that only had a volume of 128 mm^3 at an uncorrected $p < 0.005$, the smallest cluster revealed by their analysis. In addition, we calculated *d'* separately for each condition and observed that performance was lowest during the WH-LONG condition (*d'* = 2.3); this may have contributed to the lack of a distance effect for the WH-sentences (see section 2.4.2 for further discussion).

Table 2.1

Region	*Hemisphere*	*x*	*y*	*z*	*Cluster Size (mm^3)*
Main effect of distance					
Inferior frontal gyrus (*pars triangularis*)	Left	-50	16	25	656
Interaction of distance & construction					
Inferior frontal gyrus (*pars opercularis*)*	Left	-38	6	19	313
Precentral gyrus*	Left	-45	-6	20	203
Main effect of construction: BA > WH					
Anterior temporal lobe	Left	-52	0	-16	7,500
Angular gyrus	Left	-47	-63	24	5,719
Anterior temporal lobe	Right	49	9	-19	3,547
Posterior cingulate/precuneus	Left	-4	-55	27	1,297
Angular gyrus	Right	51	-63	24	891
Main effect of construction: WH > BA					
Precentral gyrus	Left	-41	-4	38	750
BA-LONG > BA-SHORT					
Inferior frontal gyrus (*pars triangularis*)	Left	-50	17	23	1000

Superior temporal sulcus	Right	50	-27	-1	890
Supplementary motor area	Left/Right	2	12	52	750

n = 25. FWE cluster-corrected $p < 0.05$, individual voxel threshold $p < 0.001$, cluster size threshold 608 mm^3.
*significant at reduced cluster size threshold (200 mm^3)

Table 2.1 lists the Talairach coordinates of the center of mass and the cluster size for each of the contrasts listed above (main effect of distance, interaction of distance/construction, main effect of construction, and simple effect of distance in the Backward Anaphora condition).

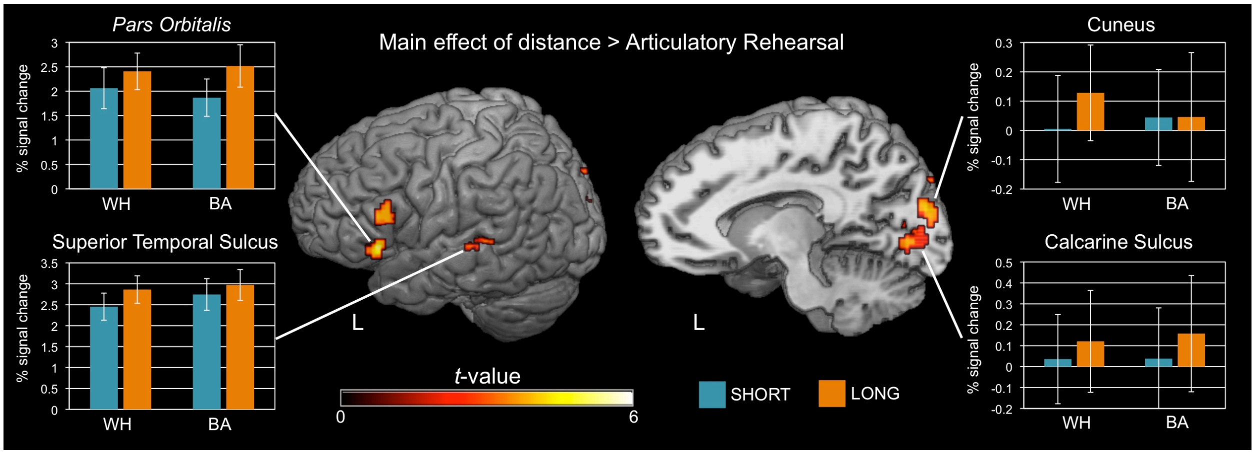


Figure 2.6. Group activation maps (*n* = 23) displayed in Talairach space on a template brain for the main effect of distance > articulatory rehearsal. Activations are shown using an individual *t*-threshold of $p < 0.001$ (one-tailed) and a cluster size threshold of 300 mm^3. Barplots indicate average percent signal change for each condition within selected clusters of activation (error bars indicate standard error of the mean).

Table 2.2

Region	*Hemisphere*	*x*	*y*	*z*	*Cluster Size (mm^3)*
Main effect of distance > ART					
Calcarine sulcus	Left	-5	-79	4	1438
Cuneus	Right	11	-84	23	719
Cuneus	Left	-9	-88	16	641
Inferior frontal gyrus (*pars orbitalis*)*	Left	-49	22	0	406
Inferior frontal gyrus (*pars triangularis*)*	Left	-52	18	19	359
Superior temporal sulcus*	Left	-56	-33	4	344

n = 23. FWE cluster-corrected $p < 0.05$, individual voxel threshold $p < 0.001$, cluster size threshold 610 mm^3.
*significant at reduced cluster size threshold (300 mm^3)

The contrast [[LONG > SHORT] > ART] from the subset of 23 subjects who performed the ART condition revealed two clusters in the vicinity of Broca's area at a reduced cluster size threshold: one in the left *pars triangularis*, and a second in the inferior portion of the LIFG in the *pars orbitalis*. In addition, the contrast revealed effects in bilateral occipital lobe and left superior temporal sulcus. Fig. 4 illustrates these effects, and Table 2.2 lists the Talairach coordinates of the center of mass and the cluster size for the activations.

2.4. Discussion

2.4.1 Distance effects for Backward Anaphora in Broca's area

Consistent with our predictions, the distance manipulation in the backward anaphora condition resulted in activity in the *pars triangularis* of Broca's area. In combination with previously reported results (Fiebach et al., 2005; Santi & Grodzinsky, 2007a; Santi & Grodzinsky, 2010), this suggests that the contributions of the *pars triangularis* to sentence processing is not specific to the syntactic operation of movement. Instead, these results suggest that the some aspect of the active prediction mechanisms involved in WH-dependencies and backward anaphoric dependencies is driving activation in Broca's area.

The question then is which aspect of these prediction mechanisms is driving the effect. The two prediction mechanisms share several functional components, such as access to grammatical knowledge/constraints relevant to licensing the dependencies (e.g., "island" constraints for WH-dependencies (Ross, 1967), and "binding" constraints for anaphoric dependencies (Chomsky, 1982)), cognitive control mechanisms required to manage the resolution of the dependencies in licensed/restricted syntactic contexts, and working memory mechanisms required to retrieve previously encountered material (either syntax-specific or domain-general). The current experiment was designed solely to tease apart the contribution of syntactic movement and active prediction mechanisms; future studies will be required to definitively tease apart the various components of the active prediction mechanisms that could be driving this effect.

Before moving on, it should be noted that two recent studies of activation in Broca's area are consistent with the hypothesis that Broca's area supports one or more aspects of prediction mechanisms. First, Pallier et al. (2011) presented sequences of 12 words to participants, and parametrically manipulated the size of the constituent formed by the word sequences from 1 word (i.e., an unrelated list of 12 words) to 12 words (i.e., a full sentence). They observed increased activation in the *pars triangularis* and *pars orbitalis* for constituents with real words, and for 'jabberwocky' conditions in which the content words in each trial were replaced by nonsense words. Pallier et al. interpret this as evidence that Broca's area is involved in syntactic structure-building independent of semantic processing. These results, however, are also consistent with our hypothesis that this portion of Broca's area activates as a result of prediction, as constituents of larger size provide more material from which to form predictions of the upcoming syntactic structure of the constituent, and thereby engaging additional processes such as working memory and cognitive control.

Second, Santi & Grodzinsky (2012) found that WH-questions with one filler and two gap locations did not result in increased activation compared to questions with one filler and one gap location:

(7a) [Which paper]$_1$ did the tired student submit __$_1$ after jogging?

(7b) [Which paper]$_1$ did the tired student submit __$_1$ after reviewing__$_1$?

Crucially, the second gap in these constructions is unpredictable (and in fact is not licensed by itself, leading to the moniker “parasitic gap” for these constructions; Engdahl, 1983). Evidence from online reading times suggest that only the first gap in these constructions engages an active prediction mechanism; the second gap does not appear to be actively predicted by the parser (Wagers & Phillips, 2009). Despite the lack of active prediction in these two-gap constructions, many syntactic analyses derive the two gap locations from two instances of syntactic movement. In this way, the syntactic movement hypothesis should predict increased activation for sentences containing two gaps, whereas a prediction-based hypothesis would predict equal activation between one-gap and two-gap sentences, as only the first gap engages prediction mechanisms in two-gap sentences. The results of Santi & Grodzinsky (2012) and the current experiment together suggest that Broca’s area supports a role in syntactic prediction rather than syntactic movement. Interestingly, Wagers & Phillips (2009) report online reading time evidence that active predictions for two gap locations are in fact made in a different type of double-gap construction known as “across-the-board” movement constructions:

(8) Phil generally dislikes [the poetry]$_1$ that *The New Yorker* reviews __$_1$ or publishes __$_1$.

Given that both gap locations are actively predicted in across-the-board constructions, the prediction hypothesis suggested here predicts that Broca’s area should be more active in (8) than in (7b). I leave this experiment to future research.

2.4.2 The lack of distance effects for WH-dependencies in Broca's Area

Although we found a main effect of distance and no interaction in the *pars triangularis* (suggesting distance effects for both constructions), closer inspection of the data revealed that the WH distance manipulation did not in fact reveal a significant cluster in this region. The fact that the WH distance manipulation did not result in activation in Broca's area was unexpected, given previous results documenting increased activation for distance effects in movement constructions (Santi & Grodzinsky, 2007a; Fiebach et al., 2005; Friederici et al., 2006b). However, it is worth noting that Fiebach et al. (2005) found a distance effect only for object-extraction and not for subject-extraction in German, suggesting that there may be more complexity to distance effects than previously thought. The materials in the current experiment differed from the Santi & Grodzinsky 2007a materials in several ways: (i) S&G manipulated distance by number of intervening noun phrases (with a combination of relative clauses and conjunction), whereas we manipulated distance with a relative clause, (ii) S&G tested three levels of the distance manipulation, whereas we tested only two, and (iii) S&G used embedded WH-questions (such that the full sentence was actually a declarative), whereas we used matrix WH-questions (i.e., the full sentence was a question). These differences suggest that what counts as distance for the prediction mechanisms, and how strong those effects are, may be an interesting area of investigation, especially given the apparent asymmetry between WH-dependencies and BA-dependencies in the current experiment. As mentioned in the results section, their distance effect was statistically tenuous as well. In addition, our behavioral data indicate that the WH-LONG condition was more difficult for subjects to process, and this may have impacted our ability to detect a distance effect in the WH condition. At any rate, the crucial test of the prediction hypothesis resided in the novel backward anaphora condition, which did not include a manipulation related to syntactic movement, but nonetheless resulted in a distance effect in the area of interest.

2.4.3 Effects of articulatory rehearsal

Activity in the ART condition did not account for the distance effect in the pars triangularis. This suggests that these distance effects are not accounted for by an articulatory component of verbal working memory. However, as discussed in Chapter 3, there are good reasons for postulating the existence of sentence-specific working memory resources, apart from domain-general working memory. In fact, other researchers have posited working memory beyond the phonological level (Caplan & Waters, 1999; Stowe et al., 2005), involved in maintaining linguistic information relevant to syntactic structure, and this might certainly account for the activations obtained in our study. In addition, a cognitive control mechanism might account for our activations as well. We did find activations to the ART condition in the more posterior and inferior parts of the LIFG (*pars opercularis*, frontal operculum) that are also reported for syntactic complexity effects (Rogalsky et al., 2008; Fiebach et al., 2005; Friederici et al., 2006b) and we agree with the conclusions of Rogalsky et al. (2008) and Rogalsky & Hickok (2011) that activations in those studies reflect verbal working memory rather than sentence processing or syntactic operations. However, I cannot make any strong conclusions from this study beyond the fact that the distance effects found in the *pars triangularis* cannot be attributed to increased demands on subvocal articulation as tested in our study.

2.4.4 Activations in the posterior temporal lobe

The distance manipulation in the backward anaphora condition also revealed activations in right posterior STS/MTG, which have been found in previous studies of syntactic distance and complexity (Bornkessel et al., 2005; Fiebach et al., 2005; Pallier et al., 2011), although we did not observe effects for these regions in the left hemisphere that are typically reported. Grodzinsky & Friederici (2006) and Friederici (2002) suggest that these areas are involved in either lexical-syntactic integration or syntactic repair. This is indirectly supported by results in the P600 event-related potential (ERP) literature. The P600 response is elicited in situations involving syntactic reanalysis and repair such as garden-path sentences and syntactic violations, as well as sentences that are syntactically well-formed but cause difficulties in syntactic integration (Friederici et al., 1996; Kaan et al., 2000; Osterhout & Holcomb, 1992). The distribution of the response on the scalp is typically centro-posterior, and may have a source in the posterior temporal lobe (Friederici et al., 2003). Other researchers have posited the superior/middle temporal lobe as part of phonological and lexical processing networks (Hickok & Poeppel, 2004; 2007; Wise et al., 2001). It is difficult to ascertain whether increased activation in these areas due to the syntactic distance manipulation reflects increased load on phonological and lexical processing, or in lexical-syntactic integration itself. Further research is needed to clarify the role of these regions during sentence processing to disambiguate these two proposals, and is beyond the scope of the present study.

2.4.5 Main effects of construction

While the effects from the contrasts [BA > WH] and [WH > BA] invite speculation, the experiment was not designed to control for differences between these conditions, which are many (backward anaphora sentences contained an additional clause in general, BA sentences contain a causal adjunct clause, the two constructions result in different prosodies, the constructions differ in lexical content, etc.). Therefore I will not attempt to draw any conclusions beyond noting that the ATL has been previously implicated in sentence processing (Humphries et al., 2005; Mazoyer et al., 1993; Pallier et al., 2011; Rogalsky & Hickok, 2009) and the angular gyrus in semantic processing (Binder et al., 2009), suggesting that the backward anaphora condition required more of both syntactic and semantic processing, while the frontal areas revealed may reflect increased reliance on working memory and/or cognitive control during the WH condition.

2.4.6 An objection to the present conclusions: sentence-selective activations in Broca's area

While the present results contribute to a body of literature suggesting a domain-general, nonsyntactic function for Broca's area in sentence processing, an interesting objection to this position comes from the existence of sentence-selective activations in Broca's area (Fedorenko et al., 2010; 2011; 2012; Hickok & Rogalsky, 2011). Essentially, these studies show that within individual subjects, there may exist subregions of Broca's area that show increased response to the presentation of sentences over lists of words, but do not respond to domain-general tasks of working memory and cognitive control. *Prima facie*, these results constitute a strong objection to the conclusions of the present study that Broca's area contributes domain-general resources to sentence processing. However, these sentence-specific activations are curious in light of the strong neuropsychological evidence suggesting that patients with damage to this region do not seem to exhibit deficits in syntactic processing (Linebarger et al., 1983; Bastiaanse & Van Zonneveld, 1998), and the results fly in the face of ample neuroimaging evidence reviewed and presented in this study indicating that activations in this area track with domain-general functions. What do these sentence-selective activations reflect, if not syntax? Chapter 3 explores this issue extensively, offering up the same answer as presented in this chapter: domain-general working memory, cognitive control, or other resources; I account for sentence-specificity by positing *neuronal retuning* of domain-general functions. I.e., the functions performed by subregions of Broca's area are domain-general working memory, cognitive control, etc., but the inputs are language-specific features or representations.

2.5 Conclusions

While a definitive answer to the question of the specific role of Broca's area will require additional studies, the results of the present study suggest Broca's area is more likely to support the mechanisms deployed during the active prediction of gap locations in WH-questions and antecedents in backward anaphora (or a related general cognitive process), and less likely to support specific syntactic operations like movement. This hypothesis is consistent both with the current result that both filler-gap and anaphoric long-distance dependencies result in activation in the *pars triangularis*, but only if the dependencies involve prediction mechanisms, and with recent studies investigating the role of Broca's area in syntactic processing (Pallier et al, 2011; Santi & Grodzinsky, 2012). Determining exactly which components of the prediction mechanisms are driving this activation, and whether the components are language-specific or domain-general will require future studies. More generally, the results are consistent with observations that activity in Broca's area corresponds to domain-general processing mechanisms rather than syntactic operations (Rogalsky & Hickok, 2011; Kaan & Swaab, 2002).

These results are consistent with a suggestion by Bornkessel-Schlesewsky & Schlesewsky (2013) in a recent review. They suggest that Broca's area is not involved in sentence comprehension directly, but that it is a mediator between non-sequential processing in the ventral stream and sequential processing in the dorsal stream, and a provider of top-down information to each stream. This is compatible with the claims of Novick et al. (2005) that the function of Broca's area during sentence comprehension is cognitive control. Within the context of the present experimental findings and distance effects more generally, demands on cognitive control may increase while holding the filler or anaphor in memory and processing additional syntactic/semantic content from the ongoing sentence during the longer conditions. Whether or not different subregions of Broca's area contribute to sentence processing beyond cognitive control and verbal working memory remains to be investigated. Finally, further research into the contribution of other areas potentially involved in sentence-level processing (e.g., anterior temporal lobe, Mazoyer et al., 1993; Humphries et al., 2001; Rogalsky & Hickok, 2009, Pallier et al., 2011) and the interaction of these networks will be critical to clarify the neural bases of syntax and sentence processing.

In the next chapter, I turn to the issue of apparent sentence-specificity of activations found in individual subjects in Broca's area (Fedorenko et al., 2010; 2011; 2012; Hickok & Rogalsky, 2011), and discuss how these results do not represent a challenge to the domain-specificity hypotheses discussed in this chapter. In addition, the discussion concerning Broca's area serves as a useful cautionary example regarding domain-specificity of neuroimaging response more generally.

Chapter 3

A neuronal retuning hypothesis of sentence-selective activation in Broca's area

As discussed in Chapter 2, the attempts to determine the neural instantiation of syntactic operations has largely focused on Broca's area, the left inferior frontal gyrus (LIFG; Brodmann areas 44 and 45). I will refer to the research program aimed at mapping the neural basis of syntactic operations as the 'search for the syntax area', or SSA. Chapter 2 discussed some of the literature underlying the SSA and Broca's area, reviewing literature supporting a domain-general function for Broca's area in sentence comprehension, consisting of working memory and/or cognitive control, rather than a role for syntactic operations. The experiment presented in Chapter 2 bore on this issue, in support of a domain-general function, by demonstrating that this region's role in the comprehension of long-distance dependencies consists of processing related to predictability, rather than to the particular syntactic operation Movement. In the current chapter, I address important objections to the domain-general positions on Broca's area regarding the findings of sentence-specificity of activations in individual subjects in Broca's area (Fedorenko et al., 2010; 2011; 2012; Hickok & Rogalsky, 2011). While these sentence-preferring activations were not accounted for by several different domain-general tasks (Fedorenko, 2012), there may be domain-general mechanisms beyond those tested that account for such apparent sentence-specificity (Hickok & Rogalsky, 2011). However, I will argue that these activations may reflect domain-general mechanisms that are partially specialized for sentences. In addition, the discussion of this issue serves as a useful point of departure for a larger discussion of the issues surrounding cortical response-specificity to particular *inputs*, rather than *computational properties* – the response of a region to a particular input is important, but given the constant possibility of *neuronal retuning*, or the development of cortical input specificity in ontology, there is little assurance that response specificity isolates the computations of interest. Assessment of response specificity is no replacement for assessment of computational properties. The ideas presented in this chapter were developed in collaboration with my thesis advisor, Gregory Hickok.

The concept of a “domain-general specialization” is not an oxymoron. An example is the visual word form area, which clearly draws on neural resources that are not pre-wired to handle written language and only written language, but rather develops out of networks that are domain-general with respect to reading but differentiates into a specialized circuit with reading experience (Cohen et al., 2000; 2003; Dehaene & Cohen, 2007; 2011). Similarly, I will argue that Broca’s area (or any portion thereof) is not pre-wired for sentence processing and only sentence processing (of any sort), but rather can develop into a relatively specialized *supporting role* for sentence processing, drawing on neural resources for domain-general processes such as cognitive control and aspects of working memory. Broca’s area, on this view, is not the “syntax area.”

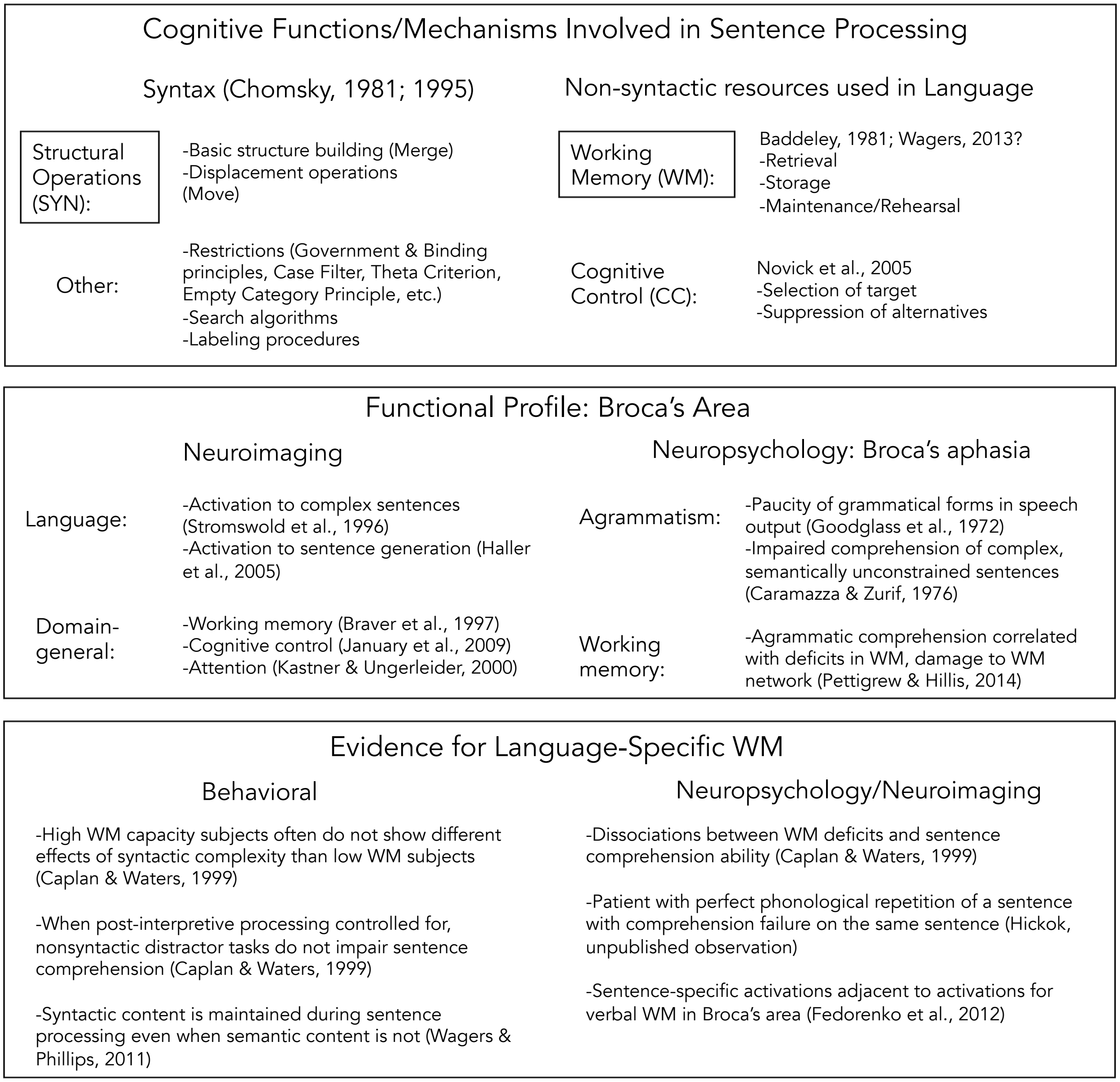
3.1 Introduction

3.1.1 Sentence selectivity in Broca’s area

A particularly relevant issue to the discussion of the relation between Broca’s area and syntax is the apparent existence of sentence-selective subregions of Broca’s area (Fedorenko et al., 2010; 2011; 2012). Fedorenko, Kanwisher and colleagues have pursued the SSA by developing a technique in functional magnetic resonance imaging (fMRI), previously used to identify a face-selective region in the fusiform gyrus (the ‘fusiform face area’, or FFA) that uses a language localizer task to identify language-responsive functional regions of interest (fROIs), then measures the BOLD response within these fROIs to various tasks or stimuli of interest. The results of these investigations have revealed that within language-responsive areas of Broca's area there are subregions that show a response profile selective to sentences (mostly in written form, see below for discussion). Such subregions show activation to sentences > lists of nonwords, but little or no activation to domain-general stimuli/tasks highlighted by domain-general hypotheses such as working memory, cognitive control, and arithemetic. Fedorenko & Kanwisher (2009) suggest that other studies did not find differences in activation in Broca's area between sentences and domain-general tasks because of variability in individual subject activation and anatomy, which blur these activation differences when group analyses are performed. By using their individual subject functional localizer, they revealed sentence-specific activations that lie directly adjacent to non-sentence activations that may have been missed in previous studies.

The existence of sentence-specific activations in Broca's area that are not reducible to domain-general working memory or cognitive control poses a problem for domain-general hypotheses of Broca's area function. Hickok & Rogalsky (2011) observed that these studies used visual materials and a probe task during comprehension, and as reading has been shown to invoke articulatory processes (Daneman & Newson, 1992), these results might be conflated with articulatory rehearsal mechanisms. Rogalsky et al. (in revision), surveyed neuroimaging studies contrasting sentence to non-sentence stimuli, showing that the majority of studies with auditory presentation do not find activation in Broca's area, while the majority of studies with written presentation do. However, the Fedorenko studies presented subjects with a verbal working memory task (presumably relying on articulatory rehearsal) that did not activate the regions activated by the sentences, suggesting that these activations do not reflect phonological working memory as measured in those studies. Alternative domain-general mechanisms, particularly those involving predictive processes, may account for these activations, as sentences contain important information about the upcoming content of the sentence (see Chapter 2 for the importance of prediction to the processing of long-distance dependencies). However, assuming the sentence-specificity found in these studies is truly sentence-specific, and Broca's area's contribution to sentence processing consists of domain-general functions, what do these sentence-selective activations reflect?

A tempting answer is syntax, as this is the highly important, sentence-specific component of language, and in accord with syntax-specific proposals. However, the presence of sentence-selective regions in Broca's area does not indicate that the function of these regions lies in syntax. Regardless of the existence of sentence-selective activations, there is good reason to posit a domain-general function of Broca's area in sentence processing: activations in this region pattern with non-syntactic processing mechanisms rather than syntactic operations, (Rogalsky & Hickok, 2011; Matchin et al., in revision, Kaan & Swaab, 2002), and patients with agrammatic aphasia and damage to this neural vicinity make grammaticality judgments successfully (Linebarger et al., 1983), and do not incorrectly produce inflected verb forms in the wrong syntactic positions (Bastiaanse & van Zonneveld, 1998), suggesting preserved syntactic competence. To resolve this issue, rather than positing a role for Broca's area as the 'syntax area', I posit that these activations reflect language-specific retuning of domain-general mechanisms, including language-specific working memory as hypothesized by Caplan & Waters (1999). Fig. 3.1 details a schematic of this argument that will be discussed in detail throughout this chapter.



Cognitive Functions/Mechanisms Involved in Sentence Processing

Syntax (Chomsky, 1981; 1995)

Structural Operations (SYN):
-Basic structure building (Merge)
-Displacement operations (Move)

Other:
-Restrictions (Government & Binding principles, Case Filter, Theta Criterion, Empty Category Principle, etc.)
-Search algorithms
-Labeling procedures

Non-syntactic resources used in Language

Working Memory (WM):
Baddeley, 1981; Wagers, 2013?
-Retrieval
-Storage
-Maintenance/Rehearsal

Cognitive Control (CC):
Novick et al., 2005
-Selection of target
-Suppression of alternatives

Functional Profile: Broca's Area

Neuroimaging

Language:
-Activation to complex sentences (Stromswold et al., 1996)
-Activation to sentence generation (Haller et al., 2005)

Domain-general:
-Working memory (Braver et al., 1997)
-Cognitive control (January et al., 2009)
-Attention (Kastner & Ungerleider, 2000)

Neuropsychology: Broca's aphasia

Agrammatism:
-Paucity of grammatical forms in speech output (Goodglass et al., 1972)
-Impaired comprehension of complex, semantically unconstrained sentences (Caramazza & Zurif, 1976)

Working memory:
-Agrammatic comprehension correlated with deficits in WM, damage to WM network (Pettigrew & Hillis, 2014)

Evidence for Language-Specific WM

Behavioral

-High WM capacity subjects often do not show different effects of syntactic complexity than low WM subjects (Caplan & Waters, 1999)

-When post-interpretive processing controlled for, nonsyntactic distractor tasks do not impair sentence comprehension (Caplan & Waters, 1999)

-Syntactic content is maintained during sentence processing even when semantic content is not (Wagers & Phillips, 2011)

Neuropsychology/Neuroimaging

-Dissociations between WM deficits and sentence comprehension ability (Caplan & Waters, 1999)

-Patient with perfect phonological repetition of a sentence with comprehension failure on the same sentence (Hickok, unpublished observation)

-Sentence-specific activations adjacent to activations for verbal WM in Broca's area (Fedorenko et al., 2012)

Figure 3.1. A schematic of the argument in favor of language-specific working memory.

In particular, the perspective offered in this chapter is that regions for language-specific working memory and/or cognitive control develop out of areas for domain-general processes in Broca's area through *neuronal retuning* (NR). Dehaene, Cohen & colleagues have postulated the notion of *neuronal recycling* to account for the apparent response specificity in the visual word form area (VWFA) for another domain of language: reading (Cohen et al., 2000; 2003; Dehaene & Cohen, 2007; 2011). Reading is a particularly striking case of neural domain-specificity, as reading cannot be a genetically encoded function, given its recent cultural emergence. Nevertheless, neuroimaging and neuropsychological studies of orthography perception has revealed the existence of this orthography-selective region in the left lateral occipito-temporal sulcus. According to Dehaene & colleagues, reading "encroaches" on pre-existing brain regions with appropriate receptive field size and suited to processing shape. Repeated exposure and cultural pressure to read early in life apparently shapes the response-selectivity of this region for reading in connection with the rest of the language network. Likewise, innate constraints on form processing in the brain constrain the development of possible orthographic systems, suggesting a limited range of possible systems to small sets of learnable symbol shapes. In this chapter, I prefer the term *neuronal retuning* as it emphasizes the important role that the computational constraints within a given brain network play in the emergence of response-specificity. That is, *recycling* implies the possibility of retooling for completely new functions (e.g., plastic bottles recycled into a fleece jacket), while *retuning* implies a relation between the old and new functions. For example, the VWFA is refined from a portion of *visual* cortex, not from, say, somatosensory cortex or the dentate gyrus. It is plausible that sentence processing, relying on domain-general mechanisms such as working memory and cognitive control in Broca's area, has led to a degree of language-specificity in this region in a similar fashion as the VWFA. Given the striking case of neuronal retuning for orthographic processing in the VWFA, it is reasonable to expect retuning in many parts of the cortex to greater or lesser extent. This is no different for language processing in Broca's area. If this is the case, then the apparent tension between domain-general hypothesis of Broca's area function and sentence-specific activations in Broca's area is resolved: sentence specific activations reflect domain-general mechanisms (e.g., working memory, cognitive control) that have been retuned for language processes, specifically, through experience. As such, the neural instantiation of syntactic operations *per se* remains at large.

I will first review the neuropsychological and neuroimaging data relevant to Broca's area, syntax, and sentence processing, and review the neuronal recycling/retuning hypothesis (NRH) in the case of the VWFA. Following this, I will review the debate over the existence of language-specific working memory resources and extend the NRH to language, working memory, and Broca's area. Throughout the review, I will adopt a relatively agnostic perspective on processing resources, including short-term storage, maintenance, retrieval, and selection within the header of working memory.

3.2 Broca's area, syntax, and domain-general processing

The interest in Broca's area as a region crucial for sentence processing began with experimental investigation into the sentence comprehension ability of patients with Broca's aphasia. Broca's aphasia is a nonfluent language disorder induced commonly through stroke, typically involving damage to Broca's area and surrounding tissue (Mohr et al., 1978, Dronkers & Baldo, 2009; Damasio, 1992). For a long time, the syndrome of Broca's aphasia was characterized chiefly as a deficit in production (Goodglass, 1968; Geschwind, 1972, Kean, 1977), with observations of limited speech output, speech errors, and the absence of prosodic contours. Additionally, patients' output typically lacks functional words and morphemes and is 'telegraphic' in style – leading to the moniker 'agrammatism', or the absence of grammatical form and content. Caramazza and Zurif (1976) demonstrated that the agrammatism in patients with Broca's aphasia (as well as conduction aphasia) underlies both production and comprehension. At this point, the association between Broca's area and syntax was born, beginning a history of interest in this area as a potential syntax area. Interestingly, the Caramazza and Zurif study found that patients with conduction aphasia and presumably posteriorly-distributed lesions, showed precisely the same pattern of "agrammatic comprehension" as Broca's aphasics, but this is rarely discussed (Hickok, 2000; Linebarger et al., 1983).

The second critical piece of evidence supporting the association between Broca's area and syntax came in the form of neuroimaging studies that showed activation in Broca's area to sentence complexity manipulations (Stromswold et al., 1996; Fiebach et al., 2005, Friederici et al., 2006b; Bornkessel et al., 2005; Makuuchi et al., 2009). For instance, Stromswold et al. (1996) presented subjects with two kinds of multi-clause sentences: center-embedded and right-branching, with center-embedded sentences known to incur difficulties in comprehension. The center-embedded sentences resulted in increased activation in the pars opercularis of Broca's area relative to the right-branching sentences. Additional studies of artificial grammar complexity (Friederici et al., 2006a; Bahlmann et al., 2008) and syntactic violations (Embick et al., 2000; Moro et al., 2001; Friederici et al., 2003) also activate Broca's area. The debate over whether these activations reflect syntactic operations vs. domain-general processing comprises the central issue in discussions over the role of Broca's area in sentence processing. I will briefly discuss specific positions in favor of a syntactic function of Broca's area, followed by discussion of the evidence against these positions (for a more extensive review, see Rogalsky & Hickok, 2011).

3.2.1 Broca's area as the seat of syntactic movement

As reviewed in Chapter 1, the bridge between the generative program in syntax and neuropsychology was most conspicuously developed by the work of Grodzinsky, who posited that Broca's area underlies the transformational component of the grammar, called in some versions of syntactic theory (Chomsky 1981) the *movement* operation. The transformational component was one of the many fundamental contributions of Chomsky's work to the theory of syntax (Chomsky, 1957; 1965). Transformational rules were key to explaining the property of apparent *displacement* in sentences, a phenomenon in which a syntactic constituent appears in a different position from its canonical one. For example, in the sentence "**which man**$_1$ did the girl push **__**$_1$?", *which man* is interpreted as the object of the verb *push*, and would normally follow the verb ("the girl pushed the man"), and a long-distance dependency forms between the filler "which man" and its canonical location, the gap. Such displacement poses challenges for theories of language in which the local syntactic structure of a representation governs its semantic interpretation (Fodor, 1975; Chomsky 1995; Marantz, 2005). Chomsky resolved this issue by positing that the grammar generates a set of "base" sentences, which govern semantic interpretation, and which are modified by transformational rules to generate "surface" sentences, which are spoken aloud (Chomsky, 1957). During comprehension, the transformational rules would be applied in reverse to allow semantic interpretation of the sentence. Later instantiations of syntactic theory, in particular *Government and Binding* (Chomsky, 1982), highlighted a single transformational rule, *Movement*, to account for displacement phenomena, with filler-gap dependencies analyzed as instances of syntactic movement. Among other revisions in the theory, this was a particularly significant step forward that unified various phenomena within the field. The unification of transformational rules under the umbrella of a single operation served as the catalyst for investigations into the sentence comprehension deficit in Broca's aphasia.

Grodzinsky based his Movement hypothesis regarding the agrammatic deficit in Broca's aphasia on observations of asymmetry in the sentence comprehension deficit in these patients. When faced with a simple sentence and canonical word order, such as "the girl pushed the boy", patients performed quite well in interpreting *the girl* as the pusher and *the boy* as the pushee of (Caramazza & Zurif, 1976). Patients also showed no difficulties with sentences with noncanonical word order (i.e., sentences with certain types of Movement) that had a clear, non-reversible semantic interpretation, e.g. "the apple was eaten by the girl". However, when faced with sentences with noncanonical word order and a reversible semantic interpretation, such as the passive "the girl was pushed by the boy", patients' performance dropped notably (Caramazza & Zurif, 1976; Grodzinsky, 1986; Grodzinsky, 2000). Thus, the very sentences that patients had difficulty comprehending were the sentences with Movement and were semantically unconstrained, suggesting a close relationship between the brain regions damaged in this syndrome and the Movement operation. Grodzinsky posited that these patients lacked the capacity to process the Movement operation, and could only guess at the correct meaning (Grodzinsky, 2000) in cases of semantic reversibility.

The data from aphasia are supported by neuroimaging studies that show that sentences with long distance intervening filler-gap dependencies activate Broca's area more than sentences with short distance (Fiebach et al., 2005; Rogalsky et al., 2008; Santi & Grodzinsky, 2007a). For instance, Santi & Grodzinsky (2007a) showed that activity in the anterior part of Broca's area, the *pars triangularis*, showed increased activity for increased distance in Movement constructions, but not for increased distance in Anaphor Binding constructions, another type of long-distance dependency. A repetition suppression study by Santi & Grodzinsky (2010) indicated that repeated presentation of structures with filler-gap dependencies decreased activation in the *pars triangularis*, while repeated syntactic structures of other types did not. The apparent selectivity of responses parallels the selectivity of deficit in Broca's aphasia, together supporting Grodzinsky's account of the role of the anterior portion of Broca's area in syntactic Movement.

While Grodzinsky & colleagues' movement hypothesis of Broca's area is a cohesive account, as discussed below, other neuroimaging data support the view that Broca's area fulfills a domain-general function such as working memory or cognitive control rather than a syntactic operation such as Movement. In addition, there are neuropsychological data that complicate the picture of the relationship painted between sentence comprehension in Broca's aphasia and Movement. One such finding is that agrammatic patients have difficulty understanding other types of sentences without movement, such as sentences with prepositions (e.g., *the block is on/under the vase*; Schwartz et al., 1980). Another finding is that agrammatic patients, predicted to have poor comprehension on passives by the Movement hypothesis, often have no deficit on passive sentences or equal deficits on actives and passives (Berndt et al., 1996). And a third contradictory result is that comprehension of a canonically ordered matrix clause of a center-embedded sentence (e.g., *The girl that pushed the boy is* tall) is also impaired in such patients (patients cannot reliably judge who is tall in the preceding example; Hickok et al., 1993).

Finally, recent conjectures in linguistic theory, if correct, may entirely eliminate Movement as an independent syntactic operation, thereby precluding the possibility of a separate neuronal mechanism for syntactic Movement (although leaving open the possibility of specialized resources to handle Movement dependencies during comprehension/production). Namely, a conjecture raised in the Minimalist program (Chomsky, 1995) is that there is a single structure-building operation, Merge, that accommodates both local phrase structure building (external Merge) and displacement (internal Merge), obviating the need for a separate transformational component in the grammar. As such, any syntactic specificity in Broca's area must be relegated to this basic structure-building operation or to some other component of the grammar. However, the unification of phrase-structure building and movement into a single operation is not widely accepted, so the Movement hypothesis is still viable (although the neuroimaging and neuropsychological data speaking against the Movement hypothesis stand, regardless).

3.2.2 'Core' syntactic operations

While Grodzinsky's Movement proposal hypothesizes a role for Broca's area restricted to the transformational component of syntax, Friederici and colleagues posit broader claims for the role that Broca's area plays in syntax (Friederici et al., 2011); namely, the hypothesis that Broca's area subserves basic structure-building operations. These claims are supported by the aphasia data cited above in addition to numerous PET and fMRI studies on sentence processing. The basic finding that sentences with complex syntax or noncanonical word order activate portions of Broca's area compared to simple sentences is an accepted finding that has been replicated many times (Friederici et al., 2006b; Makuuchi et al., 2009; Santi & Grodzinsky, 2007; Bornkessel et al., 2005; Rogalsky et al., 2008; Stromswold et al., 1996), as well as the finding of increased activation in Broca's area to sentences containing syntactic violations (Embick et al., 2000; Moro et al, 2001; Friederici et al., 2003). Friederici and colleagues have interpreted these and other results in favor of a "core" syntactic account of Broca's area, according to which Broca's area performs basic syntactic operations such as hierarchical phrase-structure building (Berwick et al., 2013), and increased activation to complex sentences or sentences with syntactic violations results from increased demand on syntactic structure-building operations.

Friederici's account also specifies a role for the posterior, superior temporal cortex in syntactic processing, particularly for syntactic reanalysis. This role is supported by data from many of the neuroimaging studies cited above that, in addition to activations in Broca's area, report increased activation in the superior and middle temporal gyri to manipulations of syntactic complexity or reanalysis (Friederici et al., 2003; Fiebach et al., 2005), and event-related potential (ERP) data showing posteriorly-distributed sources of activity associated with difficulty of syntactic integration (Friederici et al., 1996; Friederici et al., 2003; Kaan et al., 2000; Osterhout & Holcomb, 1992).

Further evidence in support of the "core" syntactic account comes from neuroimaging studies of artificial languages. In these studies, the experimenters created artificial languages, typically consisting of meaningless syllables, with grammatical properties of varying complexity. Subjects then learned the grammar of these artificial languages, and the experimenters performed neuroimaging experiments while the subjects processed "sentences" in these artificial languages. In such studies, detection of grammatical violations activates Broca's area (Musso et al., 2003; Friederici et al., 2006a; Bahlmann et al., 2008). The fact that violations of both natural and artificial languages activate Broca's area suggests a functional role not contingent on semantic processing, given that the artificial languages did not include meaningful words. In addition, the study by Musso et al. (2003) found that the activity in Broca's area patterned only with grammatical rules consistent with those of Universal Grammar (i.e., structure dependent rules), and not for rules inconsistent with Universal Grammar (i.e., linear order dependent rules), even though subjects successfully learned these rules as well. This result suggests that universal constraints on the form of grammars in language are reflected in the brain, although whether Broca's area implements such constraints (i.e., syntactic operations) or its activity indirectly reflects those constraints (e.g., working memory) cannot be determined by those data – an artificial language conforming to UG would permit the use of domain-general mechanisms normally used for sentence processing.

3.2.3 Syntactic unification

The Memory, Unification and Control (MUC) framework outlined by Hagoort and colleagues (Hagoort, 2005; Snijders et al., 2009) asserts a similar "core" functional role to Broca's area in syntactic processing as Friederici and colleagues. The key difference is that Friederici and colleagues base their hypotheses in the generative tradition (Chomsky, 1965; 1981; 1995), while the MUC account is based on a unification framework (Jackendoff, 2002). In the MUC account, lexical items with associated syntactic "frames" are stored in posterior temporal cortex, and retrieved during comprehension and production of sentences. As each word is processed, the retrieved syntactic frames are unified in Broca's area to form the updated syntactic structure of the sentence. Unification operations at the phonological and semantic level are also performed in parallel in distinct subregions of Broca's area, with domain-general control operations being executed in dorsolateral prefrontal and anterior cingulate cortex as necessary during sentence processing. Hagoort's proposal is supported by much of the same neuroimaging and aphasia literature as Friederici's, and both proposals promote similar ideas regarding the role of Broca's area and the posterior temporal cortex in central aspects of syntactic processing. However, one important difference between the proposals is that while Hagoort posits unification specifically in Broca's area, with storage in the temporal lobe, while Friederici (2011) suggests that structural processing involves a wider network, including the temporal lobe. Whether these differences are substantial or merely terminological is unclear, as unification in Hagoort's model is impossible without the stored lexical representations with their associated syntactic frames.

3.2.4 Positions advocating domain-general contributions of Broca's area to sentence processing

While few would dispute that Broca's area activates to sentence complexity, many posit the role of Broca's area in processing complex sentences to domain-general operations involved in sentence processing. Several reviews of neuroimaging and lesion studies of syntactic processing have concluded that Broca's area contributes to sentence comprehension by allocating additional resources when processing load increases rather than performing syntactic operations (Kaan & Swaab, 2002; Stowe et al., 2005; Rogalsky & Hickok, 2011, Bornkessel-Schlesewsky & Schlesewsky, 2013; Novick et al., 2005). These positions are motivated in part by the repeated observation that non-syntactic processing activates Broca's area, casting doubt on the syntax-specific hypotheses. Domain-general accounts of the function of Broca's area in sentence processing include aspects of working memory and cognitive control, reviewed below. While these are two particularly notable domain-general positions, there are other domain-general functions attributed to Broca's area such as, attention, that I will not discuss for purposes of conciseness, but are mechanisms attributable to the prefrontal cortex in the vicinity of Broca's area (Curtis & D'Esposito, 2003).

3.2.5 Working memory

As discussed briefly in Chapter 2, many authors have highlighted a role for Broca's area in working memory, suggesting that activations to complex sentences results in increased working memory demands. Here, I develop this account in more detail. Notably, simple, canonical word order sentences often show little or no activation in Broca's area (Mazoyer et al., 1993; Rogalsky et al., 2011), suggesting that this region does not perform basic syntactic computations. Hickok, Rogalsky and colleagues (Hickok, 2000; Rogalsky et al., 2008; Rogalsky & Hickok, 2011; Hickok & Rogalsky, 2011) have asserted that increased activations to complex sentences in the posterior portion of Broca's area, the *pars opercularis*, as well as comprehension deficits in nonfluent aphasia, are best explained through a verbal working memory account. Verbal working memory is the temporary maintenance of speech-mediated information (Baddeley & Hitch, 1974). The cortex in the vicinity of Broca's area is involved in speech production and is implicated as a core component of a verbal working memory network, specifically, articulatory rehearsal (Buchsbaum et al., 2001; Jonides et al., 1998; Hickok & Poeppel, 2000; Hickok et al., 2003). Complex sentences such as center-embedded constructions may induce increased activation in Broca's area in fMRI studies because subjects subvocally rehearse sentence stimuli more frequently for these complex items compared to the simpler items. As reviewed in Chapter 2, Rogalsky et al. (2008) showed that articulatory suppression interfered with comprehension of more complex sentences to a greater extent that comprehension of simpler sentences in healthy young adults. In addition, the aphasia literature indicates an association between working memory capacity and agrammatic sentence comprehension (Linebarger et al., 1983; King & Just, 1991; Caspari et al., 1998; Pettigrew & Hillis, 2014).

In fact, Miller & Chomsky (1963) pointed out that constraints on temporary storage capacity are precisely the causes of difficulty in interpreting center-embedded constructions relative to right-branching structures (see also Gibson, 1998; 2000). They observed that syntactic mechanisms would readily generate center-embedded structures, but that limitations on memory would produce the difficulty in production/comprehension and thereby these constructions would be seen rarely in natural language use. If this assertion is correct, the neuroimaging results obtained by contrasting center-embedded to right-branching sentences tax the working memory resources involved in sentence comprehension rather than the structure-building operations themselves.

A working memory account of activation in Broca's area during sentence comprehension is supported by neuroimaging data. As reviewed in Chapter 2, Rogalsky et al. (2008), in an fMRI study, demonstrated that the sentence complexity effect in the *pars opercularis*, increased activation for object-relative sentences over subject-relative sentences, disappeared under conditions of articulatory suppression, which effectively factored out the contributions of rehearsal to the activation pattern. This complexity effect in the anterior portion of Broca's area, the *pars triangularis*, did not disappear during articulatory suppression, leaving the possibility of syntactic operations in this region. However, the complexity effect in the *pars triangularis* was eliminated by a sequential finger-tapping task, suggesting that this finger-tapping task engaged whatever resources were provided to sentence comprehension in this region.

It is possible that the *pars opercularis* and/or the *pars triangularis* are engaged by a working memory mechanism beyond the articulatory-phonological level, a position we shall return to further in this chapter as an important possibility to account for sentence-specific activations in Broca's area. Caplan and Waters (1999) discuss data from psycholinguistic studies indicating dissociations in domain-general working memory capacity from sentence comprehension abilities, suggesting that there are language-specific working memory resources.

For instance, Waters & Caplan (1996) found no differences among subjects with low, medium and high working memory capacity on processing times for garden-path sentences (syntactically ambiguous sentences that result in reinterpretation, e.g. *the experienced soldiers warned about the dangers conducted the nighttime raid*). Caplan & Waters (1999) discuss several examples of this type (among other evidence), concluding that there is a separate pool of resources for sentence comprehension apart from domain-general working memory that might be localized to Broca's area.

Stowe et al. (2005) cite several neuroimaging studies in support of expanded working memory in Broca's area. These studies include those finding that unstructured sequences of words find activation in Broca's area (e.g., Stowe et al., 1999; Grasby et al., 1994; Fiez et al., 1996), supporting a nonsyntactic function. However, comparisons between activation to maintenance of word lists and complex sentences showed increased activation for maintenance of sentences (Stowe et al., 1998), indicating that working memory demands were larger in the sentence condition, even though the number of words was identical. An explanation for this finding is that working memory demands of this area increase when maintenance of incomplete phrasal structure is necessary, leading Stowe et al. (2005) to suggest a working memory function of this region that extends beyond the phonological level. In addition, although there is an association between working memory capacity and agrammatic comprehension (Linebarger et al., 1983; Caspari et al., 1998), Waters et al. (1991) presented a case of a subject with a severe working memory deficit and apraxia of speech, but relatively normal sentence comprehension abilities, suggesting neuroanatomically distinct working memory resources for sentences, which may be localized to Broca's area as suggested by Stowe et al. (2005).

More recent neuroimaging data on Broca's area and sentence processing support the expanded working memory account of Stowe et al. (2005) and Caplan & Waters (1999). For example, a neuroimaging study by Pallier et al. (2011) found that sequences of words with increasing constituent structure size showed corresponding increasing activation in the *pars triangularis* of Broca's area (among other regions). A region involved in working memory for features relevant to phrasal structure would be expected to be under increased demands as phrasal complexity increases. However, these specific data are also compatible with a role for Broca's area in syntactic operations themselves, so distinguishing syntactic operations from working memory cannot be done by this study alone.

The experiment presented in Chapter 2 provides some evidence in resolution of this issue. Recall that this experiment investigated the relationship between different long-distance dependencies (movement, anaphora) and manner of processing (active, non-active). Our experiment found that a distance manipulation in backward anaphora (active processing) results in activation in the *pars triangularis* of Broca's area previously found for movement (active processing), but not for canonical anaphora (passive processing). This indicates that distance effects for long-distance dependencies in this region pattern with processing, not whether the construction is movement or anaphora. Therefore, a domain-general working memory or cognitive control account would account for the activations, but not a syntactic account. However, activation in this region did not overlap with a separate articulatory rehearsal task, suggesting that activations in this region cannot be accounted for by phonological working memory. The activation obtained in Broca's area could reflect increased reliance on an expanded, non-phonological working memory, consistent with Stowe et al. (2004). Of course, another executive processing mechanism such as cognitive control cannot be ruled out with these data (Novick et al., 2005), discussed below.

3.2.6 Cognitive control

Another domain-general processing account of Broca's area's role in language is the cognitive control hypothesis (Novick et al., 2005; 2010), in which cognitive control is exercised in cases of syntactic ambiguity, resulting in increased activation in Broca's area. Cognitive control and working memory are similar, with the key difference being a maintenance function in working memory, and a selection function in cognitive control. For instance, cognitive control must be exercised in tasks such as the Stroop or the Flanker task requiring suppression of competing representations. In the case of the Stroop task, processing difficulty results because subjects must suppress the inappropriate activation resulting from automatic reading of the words. In the case of the Flanker task, distracting stimuli (arrows pointed in one direction) compete with the appropriate response on a given trial (target in the direction opposite the flanker arrow). Novick et al. (2005) suggested that processing sentences involves cognitive control mechanisms, accounting for increased activation in Broca's area for complex sentence stimuli. Activation to tasks involving cognitive control has been shown to activate Broca's area (Milham et al., 2003; January et al., 2009; Van Veen et al., 2001), indicating the potential validity of this hypothesis. For instance, January et al. (2009) found co-localized activation in Broca's area for a stroop task and a sentence comprehension task involving syntactic ambiguity, suggesting that the region supports a domain-general cognitive control mechanism. The cognitive control hypothesis and the working memory hypothesis make similar predictions about activation patterns in Broca's area, and it may be difficult to distinguish them. Regardless, they both point to a function in Broca's area not consisting of syntactic operations, but of domain-general processing resources.

3.3 Language- or sentence-selective activations in Broca's area

One issue in deciphering the function of Broca's area in sentence processing among these alternative hypotheses is that almost all studies rely on group effects, potentially obscuring effects that could be observed in individual subjects (Fedorenko & Kanwisher, 2009). This issue has prompted Fedorenko, Kanwisher and colleagues to take a magnifying glass to the functional specificity issue. Their basic finding with respect to this issue is that there are separate subregions within Broca's area that show increased activation to sentences relative to lists of nonwords that are localized alongside domain-general subregions that activate for domain-general mechanisms such as working memory and cognitive control (Fedorenko et al., 2010; 2011; 2012). These subregions are sentence-selective, as they do not activate to the domain-general tasks/stimuli. The authors obtained this finding by adapting the approach used in identifying the face-selective response of the fusiform face area (FFA; Kanwisher et al., 1997; Grill-Spector et al., 2004; McCarthy et al., 1997). I will briefly review the methods used to identify the face-selectivity of the FFA before returning to a discussion of the Fedorenko et al. (2010; 2011; 2012) findings with respect to sentences.

3.3.1 Response-selectivity in cortex: the fusiform face area (FFA)

Kanwisher et al. (1997) investigated the functional specificity of the FFA via two steps: (1) independent functional localization in individual subjects, and (2) detailed examination of the response profile in this region. First, they localized face-preferring responses by presenting subjects with images of faces and objects in a passive viewing condition and identifying activations greater for faces than objects. This identified a face-selective region in 12 out of 15 subjects. In subsequent, independent runs, they presented partially overlapping groups of 5 subjects who demonstrated a clear face-selective response in this region with a number of non-face conditions to determine the extent of the face-selectivity of this region. The results demonstrated a strong selectivity for face stimuli compared to the other conditions (fig. 3.2).

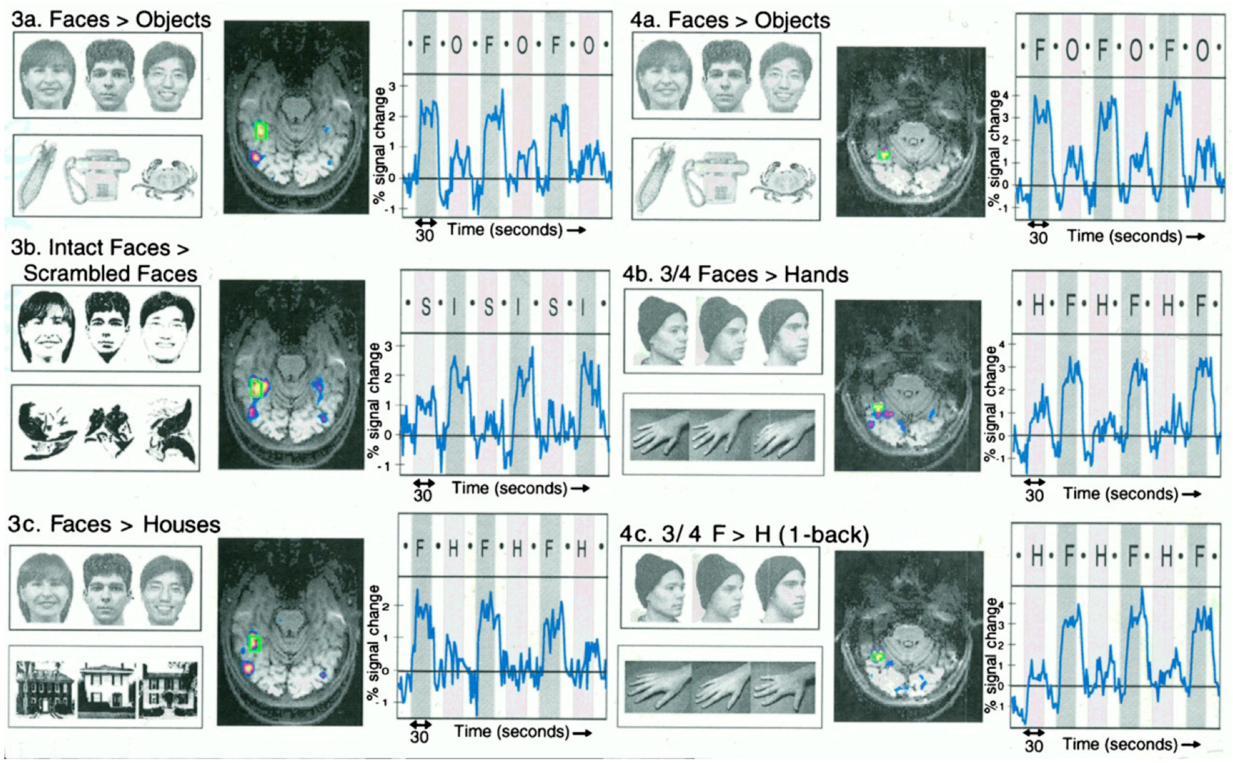


Figure 3.2 (adapted from Kanwisher et al., 1997). LEFT: five subjects who showed a clear face-selective response show increased activation to faces compared to complex non-face stimuli. RIGHT: a separate (partially overlapping) group of five subjects who showed a clear face-selective response show increased activation to faces, including spatially rotated faces, to complex non-face stimuli.

Subsequent research has confirmed the anatomical and functional specificity of the FFA. Tong et al. (2000) demonstrated that the functional response of the FFA to faces is independent of gaze orientation, and responds equally well to nonhuman faces (e.g., cats and cartoons). Grill-spector et al. (2004) found that activity in the FFA correlates with success in detection and identification of faces. Kanwisher et al. (1998) showed that the FFA shows minimal reduction of activity to inverted faces and responds well to simple grayscale and two-tone images with low visual complexity, suggesting the region is involved in face processing specifically, and not lower-level features of faces. In sum, there is a wealth of evidence supporting the existence of face-selective activations in the FFA.

3.3.2 Functional selectivity in Broca's area for sentences

Fedorenko & Kanwisher have adapted the approach used in identifying the functional properties of the FFA to language and Broca's area. First, they note that previous studies finding overlap of domain-general and sentence processing activations in Broca's area may be obscured due to group-averaging (Fedorenko & Kanwisher, 2009), particularly because of anatomical and functional variability among subjects in the inferior frontal gyrus. As such, they advocate functional localization in single subjects to avoid group-averaging effects that may have been particularly obstructive for language processing in the case of anatomical variability in Broca's area. Second, to increase statistical power, they advocate the use of functional localizers in order to precisely define language-responsive areas, and then determine if domain-general tasks of interest (e.g., working memory, cognitive control) activate these areas. Using this approach, Fedorenko et al. (2012) identified functional ROIs in Broca's area using a localizer in individual subjects, in which subjects read visually presented sentences or nonword lists and identified at the end of the sentence/list whether a probe item was contained in the stimulus. They identified language ROIs showing increased activation to sentences > nonwords, and domain-general ROIs that showed increased activation to nonwords > sentences. They then presented these subjects with various tasks, including: the stroop task, a recall task taxing working memory, music processing, sentences, and word lists. Their basic finding is that while these domain-general tasks activate subregions of the language-responsive areas, significant language-selective areas remained that appeared to show no interest in these domain-general tasks (fig. 3.3). The conclusion they draw is that language-specific and domain-general subregions of Broca's area exist side-by-side in Broca's area.

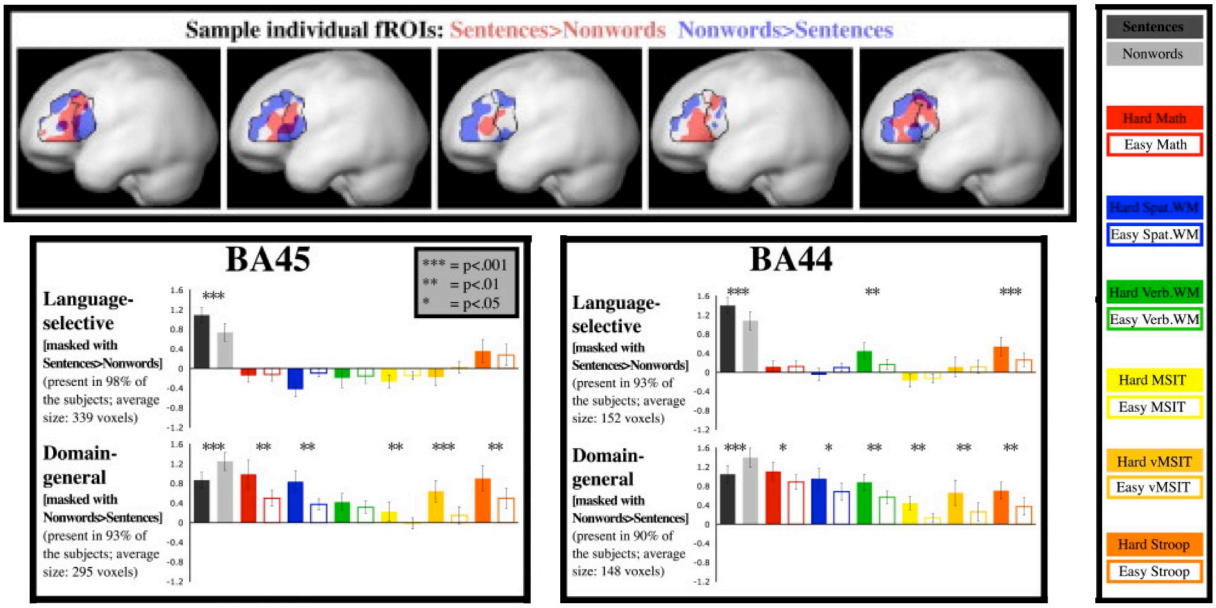


Figure 3.3 (adapted from Fedorenko et al., 2012). RIGHT: the tasks presented to subjects while in the scanner. TOP: ROIs identified by the language localizer runs. Red areas indicate regions more active for sentences than lists of nonwords (language-selective), and blue indicates regions more active for lists of nonwords compared to sentences (domain-general). Outlines of BA44 and BA45 are shown in black lines. BOTTOM: activation for each task within the identified ROIs in individual subjects. Domain-general tasks activate langauge-selective ROIs minimally or not at all, while noticeably activating the domain-general ROIs.

These findings are a puzzle for domain-general hypotheses – these positions posit that activations in Broca's area during sentence processing reflect domain-general mechanisms, but what Fedorenko, Kanwisher & colleagues have shown is that there are activations in Broca's area that *cannot* be attributed to domain-general working memory and/or cognitive control as tested in their studies. These sentence-selective activations appear to be somewhat variable, however, raising concerns to their generality with respect to some central linguistic function, such as syntax. Fedorenko et al. (2012) found some sentence-selective activation in ~90% of subjects, while Hickok & Rogalsky (2011) report individual-subject data indicating only 33% of subjects showing sentence-selective activations, and Rogalsky et al. (in revision) report ~60% of subjects with sentence-selective responses. However, the fact that at least *some* sentence-selective activations obtain requires an account for domain-general hypotheses of Broca's area function, and will be addressed below.

Regardless of whether the response profile is selective or not to sentences, the goal in neurolinguistics is to characterize the *functional networks* of the various components of language, including sentence processing and syntax, whether the response profile is selective or not to language. In other words, the fact that an area is language or sentence selective is mostly useful in light of some theory of the computations going on there. Fedorenko & Thompson-Schill (2014) in a recent review suggest that domain-specific and domain-general regions underlie the functional processing of language through their interaction in a coherent network: domain-specific brain areas form a central core of the language network, contributing proprietary, linguistic functions, while domain-general regions in the periphery of the language network contribute processing resources as needed for linguistic processing as well as for other domains. On the particular computations that language-specific regions in Broca's area contribute, Fedorenko, Kanwisher & colleagues (2010; 2011; 2012) as well as Fedorenko & Thompson-Schill (2014) remain silent, unfortunately.

Such findings are readily interpretable for researchers upholding syntax-specific hypotheses of Broca's area – presumably these language-specific activations reflect syntactic processing, as syntactic operations are the central sentence-specific components of language. However, the fact that such language-specificity is wedged directly adjacent to domain-general processing continues to raise concerns about what the function of these sentence-specific subregions actually is. In particular, sentence-selectivity does not necessarily mean syntax-specificity. The neurolinguistic goal is to appropriately characterize the function of the neural networks involved in language, whether sentence-specific or not. In light of the neuroimaging and aphasia literature reviewed above, indicating that activations in this region pattern with working memory or cognitive control mechanisms and that agrammatic patients (presumably with damage to Broca's area) have intact syntactic competence, it appears that the function of the sentence-selective regions of Broca's area is probably not syntax. If so, we are left with a paradox as to how to characterize the function of these sentence-selective subregions.

3.3.3 On response-selectivity in the cortex

It is worth considering how response-selectivity in the cortex arises. Functional specificity in cortex appears to be mediated through two interacting mechanisms, highlighted in research by Dehaene and colleagues on the visual word form area (VWFA): innate (genetic) computational constraints and neuronal recycling/retuning (Dehaene & Cohen, 2007; 2011; Dehaene, 2009). The first mechanism posits constraints on the type of inputs a cortical region accepts and the computations it performs. The second mechanism, neuronal recycling, posits that a region that is initially nonspecific to a particular input becomes functionally specialized for that input through developmental and cultural influences, within the domain of the innate computational constraints. Language, including sentence processing, is certainly a behavior that humans engage in extraordinary frequently, and barring disorder, are all experts at. Sentence processing in particular requires the use of such mechanisms as working memory to successfully build syntactic structure and assess meaning. As such, it seems likely that retuning of response properties in Broca's area has emerged through neuronal recycling. Fedorenko (2014) highlights this possibility of the sentence-specific activations obtained from her studies (pg. 6):

> Functional specialization can develop via extensive experience with particular stimuli. One notable example is the visual word-form area, vWFA, a visual region that responds selectively to letters in one's native script…Given that language is one of the most frequent and salient stimuli in our environment from birth (or even before) and throughout our lifetimes, it is computationally efficient to develop machinery that is specialized for processing linguistic stimuli.

Of course, the question remains: what specific function emerges in these functionally selective regions? Fedorenko, previously in this paper, suggested that the spatial segregation of the domain-specific and domain-general activations imply that "the computations they perform are likely to be different given their different response profiles" (pg. 5). However, the neuronal recycling/retuning hypothesis (NRH) does not indicate that any function may emerge in a given region: the computational constraints govern the type of computations that are performed. Given that domain-general processing mechanisms (e.g., working memory, cognitive control) reside in the immediate neural vicinity and the constraint stipulations of the NRH, I posit that the sentence-selective activations reflect language-specific processing mechanisms that are related to surrounding domain-general functions, chiefly working memory. Whereas Fedorenko focuses on the fact that the activations are in different houses, I focus on the fact that they are in the same neighborhood: different location, but similar character. According to this hypothesis, throughout development, language-specific neural territory is carved out of domain-general regions involved in working memory and cognitive control in Broca's area. In this particular case, I posit processing specificity for the abstract linguistic features required for sentence processing. The following section reviews the NRH discussed in the literature on the visual word form area

(VWFA) in order to fully explicate this argument for sentence processing in Broca's area, as well as discussing another potential example of neuronal recycling related to language: the human voice area (Belin et al., 2000; Andics et al., 2014).

3.4 Neuronal retuning

The underlying assumption of most researchers in cognitive neuroscience is that different parts of the brain do different things, i.e., there is functional specificity in different locations of the brain. This is not to say that functional regions are phrenological islands – rather, regions form nodes of broader networks involved in different computations. Modern-day investigations into the functional specificity of the brain have shown that this approach is justified, affirming functional specificity to different regions of the brain. For instance, the research reviewed above on the FFA demonstrates that there are face-selective regions in the visual cortex (Kanwisher, 1997; Grill-Spector et al., 2004). The specificity of the BOLD response of cortical areas appears to develop within innate boundaries genetically determined in the organism, while adapted to a certain extent to the organism's environment – dramatically so for recent human cognitive functions such as reading and mathematics (Dehaene & Cohen, 2007; Dehaene, 2009; Knops et al., 2009; Dehaene, 2011). In the case of reading, where there is repeated experience with orthography and cultural pressure to learn letters and their connection to speech sounds, there is dramatic cortical specialization for this modern cultural invention in a region known as the 'visual word form area' (Dehaene & Cohen, 2007; Dehaene, 2009). In other cases of language, such as speech perception, there appears to be some specialization for human speech in the human 'voice' area (Belin et al., 2000; Andics et al., 2014). Indeed, it may very well be the case that much of the cortex, including the FFA, undergoes environmentally-driven specialization to some degree. The hypothesis of cortical specialization for a culturally-derived function is called the *neuronal recycling* hypothesis (Dehaene & Cohen, 2007; Knops et al., 2009). In our view, the hypothesis is best viewed as the *neuronal retuning hypothesis* (NRH), given the importance of the innate computational constraints: response-specificity does not randomly develop, but follows specific guidelines of function. The following sections review the NRH in the case of reading, in light of the probable involvement of neuronal recycling in higher-level processing of language in Broca's area.

3.4.1 The visual word form area: a product of neuronal recycling

Reading is a recent cultural phenomenon, with orthography having only been invented approximately 5,000 years ago (Schmandt-Besserat, 1996). Interestingly, through a series of functional imaging studies and neuropsychological investigations, Dehaene, Cohen and colleagues have demonstrated the functional specificity for reading of a cortical region referred to as the "visual word form area" (VWFA; Cohen et al., 2000; 2002; Dehaene & Cohen, 2007; 2011). Given the extremely recent development of writing systems, it is impossible that there exists a genetic specialization for reading in the human brain; thus, any such functional specialization must come through developmental adaptation and functional plasticity. Dehaene and Cohen developed the NRH, which posits strong innate constraints on the computational nature underlying visual cognition that has directed the development of writing systems throughout history, but allows for some functional specificity to develop during development within these constraints. Cultural exposure and pressure to read are key components of this hypothesis, as the VWFA attains its reading-specific function through a re-tuning of innately specified function for combinatorial visual recognition that must be refined for reading during development.

Frith (1985) lays out the hypothetical developmental trajectory of the reading faculty that presumably accompanies this cortical retuning, recapitulated by Dehaene (2009). Underlying the child's development for reading are sophisticated capacities for visual object recognition and speech perception. Following this is a stage of phoneme and grapheme awareness, with increasing explicit recognition of phonemes and increasing recognition of letters. This stage is hypothesized to be highly interactive, and cross-linguistic research has shown that individuals learning orthographic systems without explicit representation of speech sounds do not develop strong phoneme awareness compared to those learning systems with explicit representation of speech sounds (Mann, 1986; Cheung & Chen, 2004). Finally, children reach the orthographic stage, such that orthographic forms of words are explicitly represented and may be processed without proceeding letter-by-letter, allowing parallel processing of letters to activate a word representation. Such an account is supported by data indicating that children show length effects of word recognition, while skilled readers do not (Aghababian & Nazir, 2000; Zoccolotti et al., 2005).

The neuroimaging data on the VWFA appear to corroborate this learning trajectory of a developmental specialization for visual word forms. The possibility of a cortical specialization for reading was first raised by the existence of a disorder known as alexia, a selective deficit in reading ability or letter identification (Dejerine, 1892; Binder & Mohr, 1992; Cohen et al., 2003; Damasio & Damasio, 1983). Injury to the location around the VWFA appears to be the cause of alexia (Binder & Mohr, Cohen et al., 2003; Damasio & Damasio, 1983). Dehaene, Cohen and colleagues have investigated the functional specificity of the VWFA through a series of neuroimaging experiments similar to that of Kanwisher (1997), by probing the response-specificity of the region to orthographic forms by comparing activations to comparable visual stimuli (Cohen et al., 2000; 2002; Dehaene et al., 2010). For example, Dehaene et al. (2010) examined the neural response of subjects with varying degrees of literacy to various visual stimuli, including word forms, to test the functional specificity of the region given increasing levels of exposure to written language. Letters demonstrated a significant increase of activity with increasing expertise with written language, while all other stimuli showed no relationship with literacy (fig. 3.4). Subjects with little exposure to orthography are assumed to have not undergone the critical developmental stage in which the VWFA develops its functional specificity for reading, thus exhibiting little activation in this region. Contrariwise, fully literate subjects are assumed to have fully undergone the re-wiring that accompanies constant exposure to and experience with reading. These neuroimaging findings are in agreement with the developmental account of Frith (1985), and the increased functional specialization of the VWFA presumably underlies the development of the reading faculty.

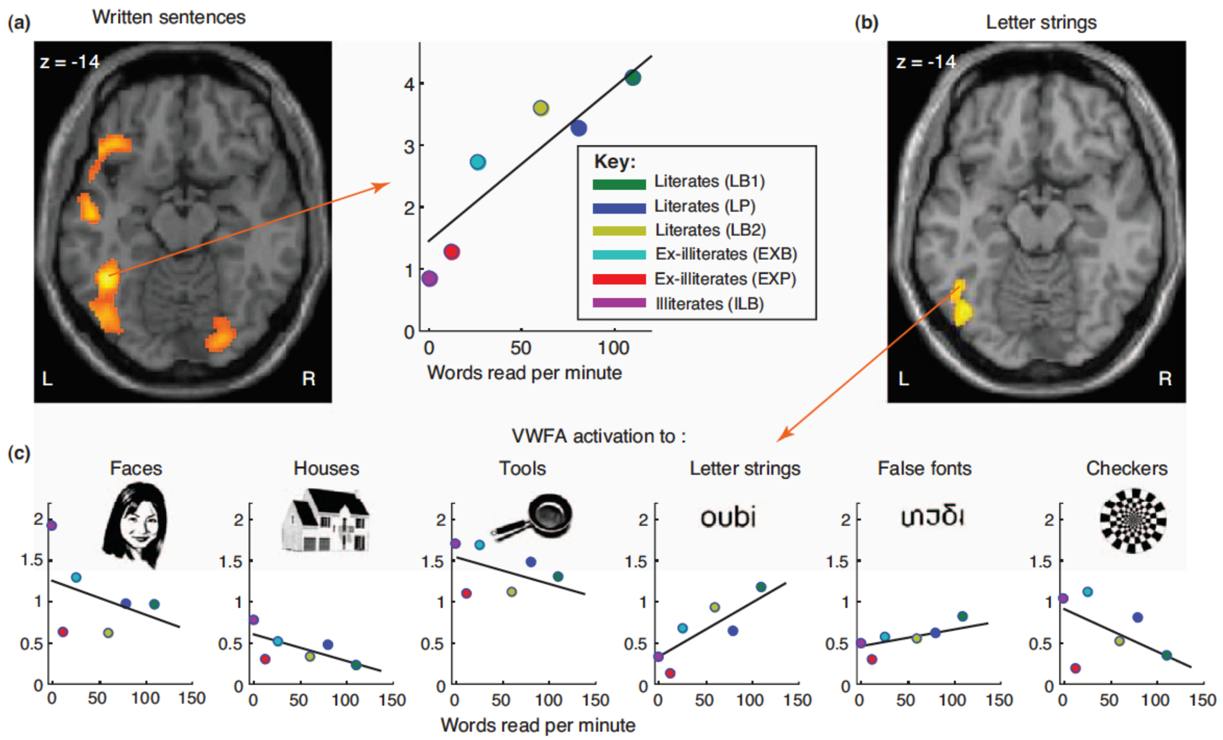


Figure 3.4 (adapted from Dehaene & Cohen, 2011, data from Dehaene et al., 2010). The VWFA activates as a function of exposure to written stimuli. (a) The magnitude of activation in the VWFA to written sentences increases as a function of literacy. (b) The VWFA activates to letter strings, and (c) does not show activation as a function of literacy for non-orthographic stimuli, but does show such a function for letter strings.

The VWFA also appears to exhibit a hierarchical organization in posterior-anterior gradient in the ventral stream along which the specificity of responses increases from equal preference to letters and nonletter control stimuli to selective preference for word-like forms (Vinckier et al., 2007; fig. 3.5). Such hierarchical activation suggests a hierarchical organization of feature detectors from basic features such as lines or conjunction of segments to letters and whole words. Such hierarchy of detectors in visual cognition is supported by single-unit data in the inferotemporal cortex of monkeys (Tanaka, 2003; Tsunoda et al., 2001).

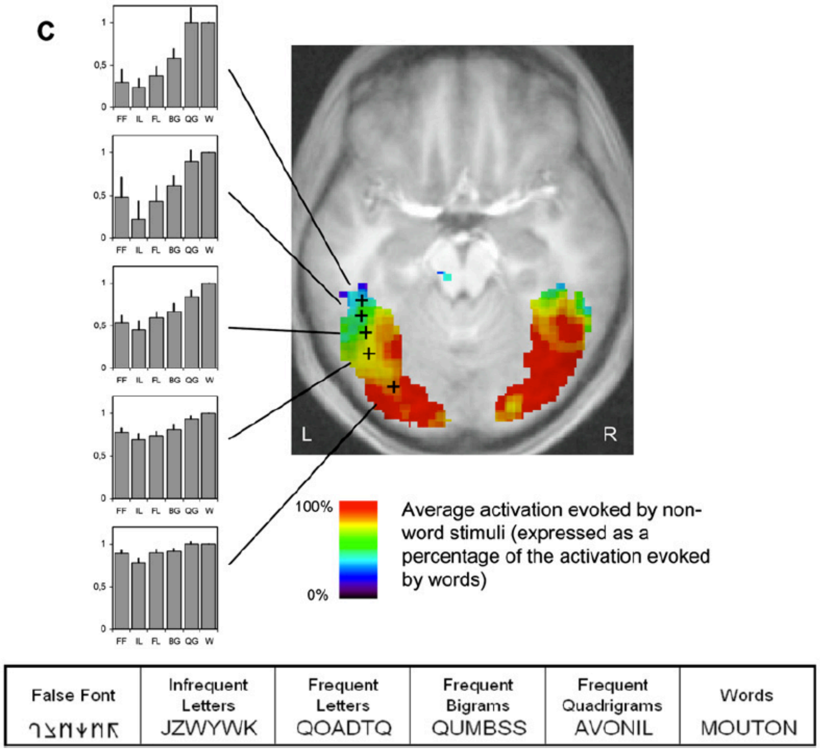


Figure 3.5 (data from Vinckier et al., 2007; figure adapted from Dehaene & Cohen, 2007). The VWFA shows increasingly specific response to readable strings along a posterior-anterior gradient in the lateral occipito-temporal sulcus.

The location and organization of hierarchical responses of the VWFA in the left hemisphere in the lateral occipto-temporal sulcus is highly reproducible across subjects, languages and experimental paradigms (Dehaene & Cohen, 2011), raising questions as to how this environmentally derived functional region finds its neuronal 'niche'. Dehaene and Cohen (2007) postulate that the location of the VWFA's consistent anatomical localization is due to three factors: (1) hierarchical activation gradient in visual cortex due to universal principles of hierarchical coding in perceptual systems, (2) position in foveal lateral occipito-temporal cortex for fine resolution of orthographic features, and (3) left hemisphere lateralization due to interaction with the rest of the language network or general analytic processing. Thus, Dehaene and Cohen highlight the importance of innate constraints on culturally derived functional maps –

such functional specificity does not appear randomly in the cortex, but finds its niche in the computationally appropriate region. Given these constraints, it is unsurprising (and, according to Dehaene & Cohen, necessary) that the location for a reading-specific function will localize to the lateral occipito-temporal cortex in the left hemisphere, as reading relies drastically on hierarchical, foveal visual form perception and phonological processing. I shall return to this point when discussing language- or sentence-specificity in Broca's area, as sentence processing relies heavily on such domain-general mechanisms as working memory, which have been shown to be an important function of the prefrontal cortex in Broca's area (Braver et al., 1997; Curtis & D'Esposito, 2003).

3.4.2 The human voice area: selectivity driven by neuronal retuning/recycling?

Reading is a cognitive faculty that everyone agrees has no specific genetic basis. As such, the apparent existence of a cortical region specialized for this faculty, the VWFA, can only be explained through an account akin to the NRH (an alternative would be denying the functional specificity of the VWFA; for this perspective see Price & Devlin, 2003; for a response, see Cohen & Dehaene, 2004). However, the extent of genetic predisposition for other cortical areas specialized for a given function is less clear. For instance, although there is likely *some* innate capacity for human speech, given that all humans use speech barring disorder, but how much is specific to processing speech itself? It may be the case that the innate computational nature of speech is not specific to it. Many researchers have highlighted the special importance of speech to the development of human language (Liberman et al., 1967; Liberman & Mattingly, 1985; Lieberman, 2000; 2002). One particularly important, human-specific capacity was thought to be categorical perception, wherein human subjects show a non-graded perception of speech stimuli within a gradient between two perceptual categories (Liberman, 1967), suggesting that subjects categorically group ambiguous stimuli onto one end or the other rather than having graded perception. Against this viewpoint, it appears that nonhuman animals can process human speech in a similar manner to humans, including categorical perception (Kuhl & Miller, 1975; Kuhl & Padden, 1982; Kluender et al., 1987), suggesting that the auditory system of humans is not substantially specialized apart from these animals.

However, neuroimaging data appear to support the "speech is special" perspective, i.e., there are regions of the human cortex in the superior temporal lobe that prefer speech to nonspeech stimuli (Wise et al., 1991; Zatorre et al., 1992; Binder et al., 1994; Price et al., 1996). In addition, it appears that human voice stimuli, whether speech (e.g., words, sentences) or nonspeech (e.g., laughs, sighs, and coughs) activate portions of the superior temporal sulcus (STS) greater than non-voice control stimuli (e.g., natural sounds, animal cries) (Belin et al., 2000). Thus, the functional specificity of the human 'voice area' suggests specialized mechanisms for the acoustic analysis of human vocalizations, akin to the specialization of the FFA for face processing.

Dehaene & Cohen (2007), after discussing the case of the VWFA, tentatively suggest that specialization for speech processing might arise from the same neuronal recycling/retuning mechanisms. They point out that the human auditory cortex is also hierarchically structured, shared with nonhuman primates (Kaas & Hackett, 2000; Pandya & Yeterian, 1990); as such, speech perception in principle could exploit neuronal recycling in the same fashion as the VWFA. Research in a nonhuman animal, the dog, regarding voice-specific responses in cortex appears to support this perspective (Andics et al., 2014). These researchers used the same technique to examine voice-specificity in humans as Belin et al., (2000), including human voice stimuli with variable emotional valence (e.g., laughing, coughing, screaming) and non-voice stimuli; but included a third category of dog vocalizations, ranging in emotional valence as well (e.g., barking, excitement whines, panting). The researchers ran both human and dog participants in fMRI and uncovered conspecific-specific activations in both species (fig. 3.6). Important to the discussion on neuronal recycling, in humans, the voice-specific regions in the middle and posterior STS preferred dog vocalizations to the non-vocal control stimuli, suggesting that these regions are not strictly conspecific specific, but tuned to familiar sounds more generally (fig. 3.6). I.e., since humans have had relatively frequent exposure to dogs, and the content of dog vocalizations is behaviorally relevant, the 'voice' area has adapted to process dog vocalizations to some degree. Thus, at least for these middle and posterior regions, functional specificity appears to be driven by development, satisfying a critical desideratum for the NRH.

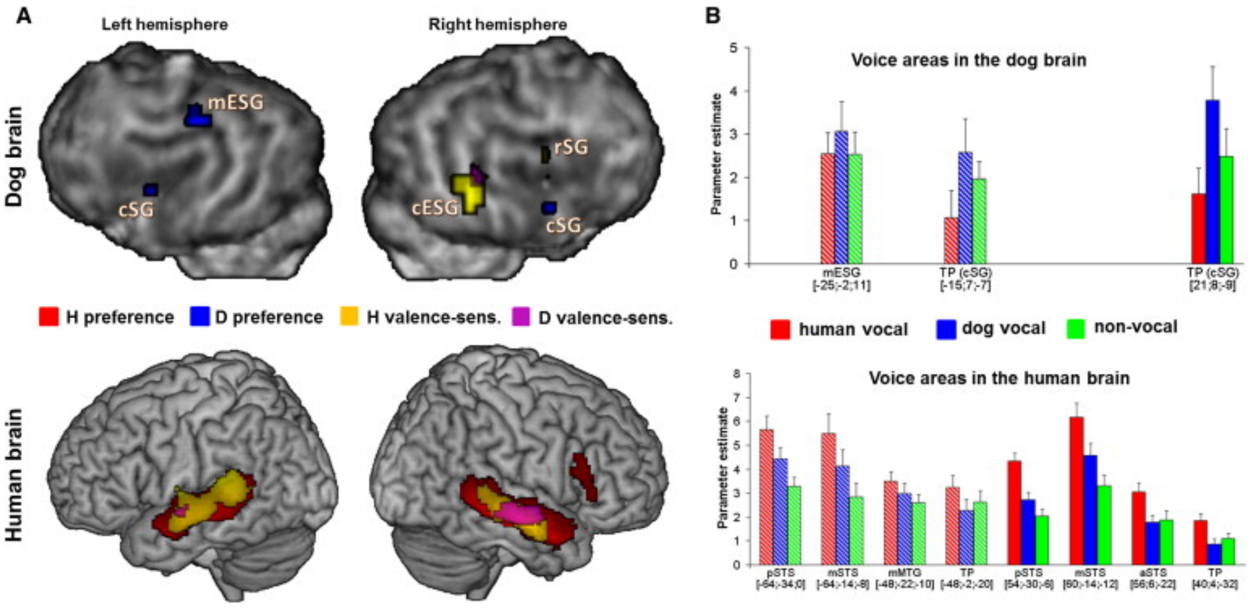


Figure 3.6, adapted from Andics et al., 2014. Both humans and dogs show response-specificity for conspecific vocalizations. (A) Activation maps displaying conspecific specific activations. (B, top) Activation in the dog voice areas prefers dog vocalizations to all other vocalizations, with no preference to human vocalizations over non-vocal sounds. (B, bottom) Activation in the middle and posterior human voice areas indicates a preference for dog vocalizations over non-vocal sounds, while anterior regions do not show this preference.

These findings are consistent with many examples of functional specialization in cortical responses, such as retuning in auditory, visual, and somatosensory cortex (Bakin & Weinberger, 1990, Diamond et al., 1999; Super, 2002). For instance, Bakin & Weinberger (1990) demonstrated that neurons in primary auditory cortex of guinea pigs exhibited receptive field tuning shifts to the frequency of tones associated with fear conditioning, while a control group with equal auditory exposure but no fear conditioning did not exhibit such retuning. These and related findings highlight the role that neuronal retuning may play a role for basic cognitive functions that clearly have a strong genetic basis, e.g. basic sensory processing, not just obviously culturally derived functions like reading. If there is retuning in basic sensory cortex, driven by cognitive and behavioral demands, there is good reason to believe there would be significant retuning in higher-level cognitive cortex, including the prefrontal cortex and Broca's area, for highly frequent and demanding functions such as language.

3.5 The neuronal returning hypothesis applied to sentence processing, working memory and Broca's area

The neuroimaging and neuropsychological evidence converge to indicate that reading, a novel capacity without any dedicated genetic basis, has a functionally specific home in the VWFA. Additionally, it is possible that another component of language, speech perception, involves neuronal retuning, accounting for human voice-specific responses in the temporal lobe. Given apparent sentence-selective activations in Broca's area, an important question for neurolinguists in characterizing the function of language networks is whether or not neuronal retuning occurs for language in this region. The NRH has two key criteria: (1) the retuned function must fit within pre-existing computational constraints, and (2) anatomical localization is contingent on the nature of the recycled function and the computational constraints. The following section addresses whether language-specific activations in Broca's area fulfill these criteria. First, I will discuss the computational nature and requirements of working memory for language with respect to other domains. Following this, I will discuss the localization evidence indicating that language-specific activations fall adjacent to those for domain-general working memory, as well as the relevant neuropsychological literature bearing on the relationship between working memory and sentence comprehension.

3.5.1 Working memory during sentence processing satisfies the computational constraint of the neuronal retuning hypothesis

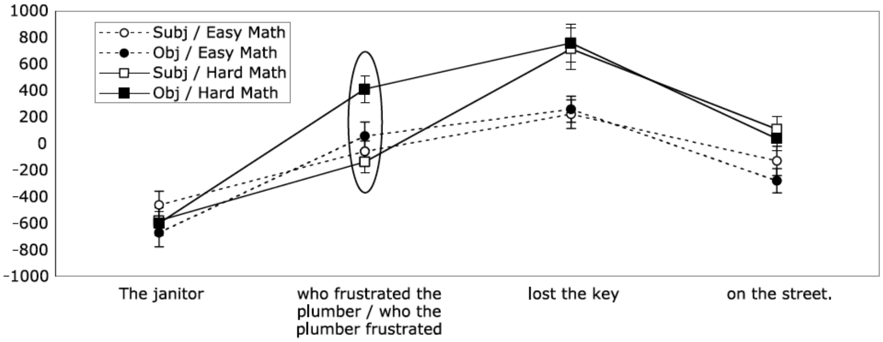
The computational constraint of the NRH posits that the retuned function must be an adaptation of pre-existing functional capacities. For instance, reading orthography is a special case of foveal visual hierarchical object perception. In the case of working memory, this means that the mechanism involved in language must be similar to that used in pre-existing domains. As is detailed below, the nature of working memory appears to be quite similar across modalities. Miller (1956), in the seminal paper *The magical number seven, plus or minus two: some limits on our capacity for processing information*, illustrated that the storage capacity of perceptual judgments among different domains is along the same order of magnitude, including perception of tone pitch (Pollack, 1952), tone loudness (Garner, 1953), taste (Beebe-Center et al., 1955), visual location (Hake & Garner, 1951), and color (Halsey & Chapanis, 1954), among others. Although the terminology "working memory" was not in use at the time, the measured channel capacities are equivalent to measures of working memory capacity. Further work explicitly characterized the notion of a “short-term store”, a singular component responsible for the storage and maintenance of temporary information across all domains (Atkinson & Shiffrin, 1971).

Baddeley & colleagues postulated the division of working memory into subcomponents and its role in sentence processing. Baddeley & Hitch (1974) proposed a tripartite division of working memory: the phonological loop, the visuo-spatial sketchpad, and the central executive. Their account was motivated through experiments indicating that a distractor task, maintaining a sequence of digits, did not have severe impacts on performance of other tasks. As such, a division of the short-term store into two components accounted for the ability of subjects to simultaneously perform such tasks. The role of the phonological loop in sentence comprehension was supported by evidence that concurrent articulation interferes with the detection of word-order violations (Baddeley, 1981) and successful comprehension of sentences (Gordon et al., 2002; Rogalsky et al., 2008). Consistent with these accounts, working memory resources required of sentence processing appear similar to other domains, as both syntactic processing (Gibson, 1998) and the N-back task (Jaeggi et al., 2003), in which non-sentence material must be maintained and rehearsed, exhibit locality costs: the more intervening material over which the information must be retained, the more difficult performance becomes.

While there is clear alignment between maintenance and retrieval operations employed during sentence processing and domain-general working memory, there appears to be conceptual and empirical motivations for language-specific working memory resources (Caplan & Waters, 1999; Wagers, 2013). Conceptually speaking, Wagers (2013) discusses possible working memory architectures in language, postulating the likelihood that language comprehenders assemble retrieval structures particularly suited to linguistic features. In particular, successful language comprehension involves the maintenance of syntactic features idiosyncratic to language. As discussed in section *3.2.5*, Caplan & Waters (1999) review behavioral data indicating that there are no differences among subjects with low or high working memory capacity and sentence comprehension. Further empirical data suggest that although semantic information may not be maintained in working memory, at least coarse-grained syntactic features appear to be (Gibson, 2000; Wagers & Phillips, 2013). Wagers & Phillips (2013) found that the filled-gap effect, the processing slowdown that occurs when an anticipated gap location is unexpectedly filled by another word (Crain & Fodor, 1985; e.g., *the general that the soldier killed* ***for*** *__ during the war ordered the invasion*) is preserved when there is extended length between filler and gap, while the semantic plausibility effect, the processing slowdown that occurs when the filler does not semantically match the verb (Traxler & Pickering, 1996; e.g., *that's the garage with which the heartless killer shot the hapless man __ yesterday afternoon*) is only weakly preserved with distance. It appears that the working memory mechanism in language is adapted for maintenance and retrieval of features most useful for successful sentence comprehension, such as syntactic features. Wagers (2013) and Ericcson & Kintsch (1995) discuss the plausibility of reconfiguration of memory and retrieval processes in language by making an analogy to expert chess players – such players can quickly and accurately remember particular board positions because of effective organization of retrieval structures. Given the extreme frequency of language use among humans, it appears that there should be some language-specific reorganization of working memory to improve performance, whether specific to retrieval or maintenance components of the system.

Data from neuropsychology also support the language-specific working memory position. Waters et al. (1991) tested a patient with preserved sentence comprehension, but strongly impaired working memory, suggesting that domain-general working memory is not strictly necessary for sentence comprehension. Another study by the same group (Caplan & Waters, 1996) illustrated that the sentence comprehension deficits in agrammatic patients were not affected by secondary working memory tasks (these patients were above chance, so this is not due to floor effects). Caplan & Waters (1999) review the data suggesting the interference of articulatory rehearsal on sentence comprehension and postulate that there is only interference when post-interpretive processing is required rather than mere comprehension of the sentence. Finally, Gvion & Friedman (2012) tested a group of Hebrew-speaking patients with conduction aphasia, with severe phonological working memory deficits, on a series of sentence comprehension tasks, which required maintenance of either semantic or phonological information. Patients were highly successful at assessing the plausibility of sentences like *this is the* ***bread*** *that the man wants that the child will* ***drink****,* requiring the maintenance of semantic content, and showed no differences between comprehension of sentences with long vs. short memory demands. However, they showed substantial impairment when performing tasks requiring long distance phonological maintenance of information, such as detecting whether the critical words rhymed in sentences such as *Hu kara harbe al* **gvura***, ve-hevin she-ze lo metuxnan tamid me-rosh, pashut ze kore kshe-en* ***brera*** (61% for patients, 89% for controls), as compared to sentences only requiring short distance maintenance, such as *Ha-xayelet hifgina* **gvura***, ki lo hayta* ***brera*** (91% for patients, 98% for controls). The results indicate a dissociation between phonological maintenance and non-phonological maintenance, supporting the existence of language-specific working memory resources that were intact in these patients.

Other authors argue against sentence- or language-specific working memory, citing behavioral data (Fedorenko et al., 2006; 2007) indicating that non-sentential distractor tasks, such as concurrently performing math problems, increase the processing slow-down of sentence reading times due to syntactic complexity (fig. 3.7, top), which the authors interpret as indicating that performing math problems requires WM resources that would otherwise be used for handling syntactic complexity. While it seems clear that nonsyntactic factors affect reading times, it is difficult to show that this indicates the complete absence of sentence-specific resources. In addition, these effects are restricted to reading times, with no effects on accuracy of comprehension (fig. 3.7, bottom). It seems that the larger pattern indicates dissociations between sentence comprehension abilities and non-linguistic working memory, suggesting *some* differentiation between processing resources in language and nonlinguistic working memory.



Arithmetic complexity	Syntactic complexity	
	Subject-extraction (Easy)	Object-extraction (Hard)
Easy arithmetic	78.6 (2.5)	74.4 (2.4)
Hard arithmetic	76.1 (2.3)	76.9 (2.6)

Figure 3.7 (adapted from Fedorenko et al., 2007). TOP: reading times in each region for each condition. At the critical region determining sentence complexity, the more complex sentence (object-extraction) shows a slowdown only during the difficult secondary arithmetic task. BOTTOM: the interaction effect found for reading times does not generalize to accuracy of comprehension; object-extracted sentences were equally difficult regardless of secondary task.

To recap, the data suggest that the computational nature of working memory for sentence comprehension is similar to that of other domains, and there is an association between working memory capacity and sentence comprehension, but there appear to be dissociations between domain-general working memory capacity and the resources required for sentence comprehension. It seems that a resolution to this situation is provided by the NRH: language-specific working memory emerges from domain-general working memory, supporting a close association in terms of computational properties while providing separate pools of resources. Given that developmental factors are key in determining the extent of domain-specificity derived through neuronal retuning, this may help explain some of the discrepancies in evidence for or against language-specific working memory, as different individuals may have developed different degrees of sentence-specific working memory resources, accounting for variability in sentence-selective responses across studies (Hickok & Rogalsky, 2011; Rogalsky et al., in revision). For instance, Rogalsky et al. (in revision) found sentence-selective responses for sentences (auditory presentation) > word lists or sentences > articulatory rehearsal in only 40-60% of subjects. If these sentence-selective activations in Broca's area form a core part of the language network (i.e., syntax), one would expect consistent sentence-selectivity; however, if these activations reflect neuronal returning of working memory, then one would expect such individual variability. I next turn to the issue of anatomical localization demands of the NRH for working memory.

3.5.2 Language-specific activations satisfy the localization demands of the neuronal recycling hypothesis

Let's assume that the agrammatic comprehension deficit of patients with Broca's aphasia stems from impairment of sentence- or language-specific working memory resources. Sentence comprehension deficits are correlated with deficits of domain-general working memory as indicated by performance on such tasks as the digit span (Linebarger et al., 1983; King & Just, 1991; Caspari et al., 1998; Pettigrew & Hillis, 2014). This is a large piece of evidence that drives the account of the domain-general hypotheses of Broca's area's function during sentence processing – that the deficit in general working memory *explains* the deficit in comprehension (Rogalsky & Hickok, 2008; 2010; Hickok, 2000). However, as reviewed above, sentence comprehension resources appear to dissociate from domain-general working memory. To resolve this paradox, note that the NRH posits that domain-specific functionality emerges in the computationally appropriate regions. Sentence- or language-specific working memory resources are, as such, likely localized *directly adjacent to* or *intermixed with* domain-general working memory resources in the vicinity of Broca's area and the prefrontal cortex more generally. Thus, a patient with damage to this general area is likely to have impairments on *both* domain-general and sentence-specific working memory, and activations to sentence processing will appear very close to activations for domain-general working memory. This accounts for the correlation between agrammatism and impairment on measures of working memory capacity such as the digit span and the general overlap of activations to working memory/cognitive control and sentence processing in Broca's area in the literature.

The data from Fedorenko, Kanwisher and colleagues (2012; 2013) indicate that, in fact, sentence-selective activations are nestled directly adjacent to domain-general activations for working memory and cognitive control. This is quite an important point – the sentence specific areas do not occupy arbitrary spatially distinct regions from working memory and cognitive control. This raises suspicions about their function, and supports the localization demands of the NRH – in the case of the occipito-temporal cortex, each stimulus-specific subregion falls under the rubric of hierarchical visual perception; in the case of Broca's area, both domain-general and sentence-specific activations fall under the rubric of working memory and cognitive control, as asserted here. With this spatial organization, it is theoretically possible for patients to have damage restricted to areas involved in domain-general working memory (e.g., the patient reported by Waters et al., 1991) or patients who have damage to both sentence-specific and domain-general working memory, resulting in both sentence comprehension deficits and impairments on measures of working memory (Caspari et al., 1998; Pettigrew & Hillis, 2014).

One residual issue is the fact that Fedorenko et al. (2012) found sentence-selective regions that showed notable activation to their nonword list condition as well, even in the near absence of activity during the verbal working memory tasks. What does the activation to their nonword condition reflect, if not domain-general working memory? Fedorenko et al. (2012), Fedorenko & Thompson-Schill (2014) and Fedorenko (2014) do not discuss this data point. Both a syntax-specific hypothesis and the neuronal retuning hypothesis can plausibly account for this finding. It appears to be the case that the nonword list conditions contained some salient similarities to sentences. The nonword lists in their experiment were scrambled versions of jabberwocky sentences, with occasional real functional words and morphemes and nonwords that are plausibly words (e.g., BOKER DESH HE THE DRILES LER CICE FRISTY'S), suggesting that language-specific resources were deployed to some degree upon encountering real functional words/morphemes and treating nonwords as new lexical items. This is consistent with the findings of Pallier et al. (2011) of activations patterning with constituent size for both real and jabberwocky sentences in Broca's area.

3.5.3 Some developmental consequences and tests of the neuronal recycling hypothesis

How would language-specific working memory develop out of domain-general working memory? In addition, what are ways to further test the NRH? I offer only a brief sketch here.

Assuming a domain-general working memory system early in development, the retrieval and/or maintenance systems would be not be specialized for linguistic input, but called upon to process sentences and abstract syntactic features such as case, agreement, etc. After repeated processing of sentences, a portion of the system would retune for the maintenance and/or retrieval of linguistic features in accordance with Wagers (2013), accepting only these features as inputs and forming proprietary connections with regions involved in access to the relevant representations. As such, sentence processing would be facilitated, as these relevant features would have proprietary access to the working memory system, and would be quickly integrated into the structure of the sentence.

This conjecture makes the same predictions as the VWFA with respect to degree of exposure to language processing. In particular, one would expect an infant to have less language- or sentence-specific cortex that would increase throughout development. Unfortunately, given the ubiquity of frequent exposure to language, it is difficult to replicate the experiments showing a relationship between activation intensity and exposure to orthography for sentences (Dehaene et al., 2010). However, it may be possible to test this hypothesis with cross-linguistic research, as there may be differences among languages with respect to the frequency of particular constructions contingent on specific linguistic features, resulting in potential activation differences in the vicinity of Broca's area.

Another prediction of the NRH is that there may be costs to neural specialization for a particular function. Dehaene (2005; 2011) notes that this may be the case for reading, that the neural territory carved out for the VWFA may result in subtle deficits in visual processing of other forms that would have had more resources to draw upon. These costs may be difficult to assess, but if found, provide evidence for the neuronal retuning view. For instance, in visual object recognition, Gauthier et al. (2003) found that expertise for the recognition of cars interfered with face recognition. The visual recognition of cars is known to engage the infero-temporal cortex close to the FFA, and activation for faces in the FFA was reduced for car experts. For language, this is a more difficult test due to universal frequent exposure to language as noted above. However, it may be possible to determine if there are correlations between facility in sentence processing and extent of language-specific activations in the vicinity of Broca's area.

3.5.4 Implications of neuronal retuning for cognitive neuroscience and the SSA

The NRH is consistent with the possibility that neuronal recycling occurs for many components of language (e.g., speech perception, reading). In general, given neuronal recycling for various components of language (reading, speech perception, working memory), it may be the case that neuronal retuning is the rule rather than the exception – that innate computational constraints allow the development and adaptation of the cortex to particular environments and functions, providing a guide to further investigations into cognition and the brain both for language and other domains. In particular, it is important to not only keep in mind that while different domains may be functionally independent and isolated from one another, i.e., modular (Fodor, 1983; Mahon & Cantlon, 2011), this does not mean they do not share similar or even identical computational mechanisms. In fact, given the prevalence of exaptation in evolution (Gould & Vrba, 1982; Fitch, 2010), or the repurposing of old mechanisms for new functions, cognitive domains likely share many underlying functional computations. Compounding the issue is that there is not only evolutionary exaptation, but also neuronal retuning (developmental retooling) of pre-existing functions, as I have reviewed in this chapter for reading, working memory, and primary perceptual processing. Clarification of the particular computational purposes of neural networks, the job of cognitive neuroscience, requires accounting for neuronal retuning.

In light of these observations, the search for the syntax area (SSA) will have to move beyond language-selective responses studied in the fashion of the FFA. These activations by themselves do not provide insight into the function performed by such selective responses, and may reflect many functional contributions involved in language and specialized for linguistic representations, but not the core computations of interest: syntactic operations. In fact, only searching in sentence-preferring areas that do not activate to other tasks may preclude the investigation into brain areas that are involved in syntax, but happen not to show a sentence-selective response. The key will be appropriate experimental designs taxing the functions of interest and dissociating these from other, nonsyntactic processes, with additional important considerations from the aphasia literature and neuroanatomical architecture, and a deeper understanding of the basic mechanisms involved in syntax revealed through linguistic research.

3.6 Conclusions

The faculty of language is perhaps the most fascinating domain of human cognition, and one of the most challenging for cognitive neuroscience. The neural instantiation of syntax, the core component of the faculty of language, has proven particularly difficult to characterize. I have reviewed the ‘search for the syntax area’, which has time and again highlighted the importance of Broca’s area as the potential locus for syntactic operations, and reviewed strong evidence against a role of Broca’s area in syntax: activations pattern with domain-general mechanisms, and the aphasia literature suggest deficits in processing but not in syntactic competence.

Attempts to further progress in this area by searching for domain-specificity, the approach taken by Fedorenko, Kanwisher & colleagues (2010; 2011; 2012) akin to the approach used in identifying the fusiform face area, fall prey to a fallacy that response-selectivity reflects independent computational properties. As research on the orthography-specific responses of the visual word form area shows, in addition to voice-selective responses in the human voice area and other examples of domain-selective responses, domain-specificity often reflects developmental retuning of particular computations for different inputs rather than independent computations. In particular, sentence-preferring activations in Broca's area likely reflect domain-general working memory retuned for the processing of linguistic representations.

Further progress in the characterization of the syntax-brain relationship will require moving beyond the assumption of the existence of a "syntax area" in the cortex, and instead focus on integrating research in formal linguistics regarding syntactic operations with work in psycholinguistics characterizing the on-line processing of sentences in production and comprehension, and taking advantage of other cognitive domains and experimental paradigms that will tap syntactic operations. As always, appropriately interpreting data from neuropsychology in light of linguistic representations and processing is critical. In Chapter 4, I discuss our attempts to do exactly this in gaining further understanding of the relationship between syntax and the brain, implementing a 'syntactic perturbation' paradigm during speech production in fMRI.

Chapter 4

Sentence production and syntactic perturbation

In Chapters 2 & 3, I reviewed the association between Broca's area and syntax, presenting empirical evidence and discussion arguing against a syntactic function for this region. Chapter 3 highlighted the obstacles in attempting to localize syntactic operations through the use of sentence-selectivity of response profile; given the persistent possibility of neuronal retuning, or developmental input-specificity, selectivity of neuroimaging response in a region does not necessarily indicate that the region performs the function(s) of interest (e.g., sentence-specificity does not imply syntax, or equivalent sentence-specific functions). The traditional cognitive neuroimaging approach is to define a task that is assumed to tap the function in question and search for brain areas that activate to that task, keeping in mind and testing alternative hypotheses that could account for the activation. Research undertaken in studying the contribution of Broca's area to syntax has generally followed this approach – researchers have employed manipulations of such variables as syntactic complexity (Stromswold et al., 1996; Friederici et al., 2006; Bahlmann et al., 2008; Santi & Grodzinsky, 2007b), syntactic violations (Embick et al., 2000; Moro et al., 2001; Friederici et al., 2003), and distance between dependent elements of a sentence (Fiebach et al., 2005; Santi & Grodzinsky, 2007a; Makuuchi et al., 2009). These researchers have sometimes made reasonable assumptions concerning the relationship between their manipulations and demands on syntactic processing, and interpreted activation in neuroimaging studies corresponding to their manipulations as indicative of syntactic processing. In addition, several researchers have generated and tested important *alternative* hypotheses regarding the function of Broca's area, such as working memory (Rogalsky et al., 2008; Matchin et al., in revision), cognitive control (January et al., 2009), and argument linearization (Grewe et al., 2006), and concluded that these alternative hypotheses provide a more plausible account of Broca's area function.

In the present chapter, I discuss our efforts to localize syntactic operations by the same methods, in sentence production – we chose a novel manipulation, based on plausible assumptions about the nature of syntactic processing and the ramifications of our manipulation on it, and obtained activations in fMRI associated with our manipulation. Importantly, I will keep in mind alternatives that may account for these activations. The present study was carried out in collaboration with my thesis advisor, Gregory Hickok.

Our manipulation consisted of syntactic target perturbation during sentence production, i.e., requiring subjects to update their syntactic plan mid-utterance, and a control condition consisting of the production of unstructured word lists. We obtained activations for syntactic perturbation in a network similar to those obtained for target perturbation during action inhibition, response selection, and motor control (neural networks commonly activated by go/no-go tasks and motor control perturbation), including subcortical structures and medial frontal, right inferior frontal, and inferior parietal cortex (Simmonds et al., 2008; Tourville et al., 2008; Diedrichsen et al., 2005; Suminski et al., 2007). Given some theoretical similarities between motor control and syntax, our results may indicate similar neural organization of syntax and motor control, but may instead only reflect increased demands on motor control itself, as syntactic perturbation presumably affected phonological/articulatory planning as well as syntactic planning, requiring future research to clarify. Syntactic perturbation particularly activated the right IFG, previously posited to be involved in action inhibition (Aron et al., 2003; 2014), while perturbation during the production of unstructured word lists did not activate, or minimally activated, this region. The fact that demands on action inhibition were stronger in the sentence condition involved syntactic structure suggest that production of utterances with syntactic structure allow more phonological/articulatory planning than production of unstructured lists. Finally, our manipulation further confirmed that the traditional candidates for syntactic processing, Broca's area and the anterior temporal lobe (ATL), did not exhibit response profiles during our experiment consistent with syntactic operations, but our results do suggest a possible role for combinatory semantic processing in the ATL, bilaterally, given that the ATL exhibited increased activation for sentences and word lists.

4.1 Introduction: Syntax & the brain so far

Before discussing the details of our attempt to localize syntactic operations through the present experiment, I will review two aspects of the current state of the field with respect to syntax, sentence processing and the brain that were not extensively reviewed in the previous chapters; namely, I will discuss the literature surrounding the anterior temporal lobe, or ATL, particularly its canonical finding of increased activation in PET and fMRI studies to sentences over word lists, and the literature on sentence production and neuroimaging. For discussion of Broca's area and syntax, see Chapters 2 and 3.

4.1.1 The anterior temporal lobe & combinatory processes

Putting aside Broca's area, the other prominent candidate for the locus for syntactic operations in the neuroimaging literature is the anterior temporal lobe (ATL). Evidence for this position is chiefly comprised of the observation that sentences activate this region more than lists of words (Mazoyer et al., 1993; Humphries et al., 2005; 2007; Vandenberghe et al., 2002;

Rogalsky & Hickok, 2009), among other neuroimaging results demonstrating an association between combinatory processing and activation in the ATL (discussed below). The assumption of the sentence > word list result is that the comprehension of sentences involves the building of syntactic structure, while the perception of non-sentence word lists does not involve syntactic structure building. With this assumption, increased activation in PET or fMRI in the ATL to this contrast may reflect syntactic operations. Of course, there are a number of possibilities to account for this activation, e.g., processes related to semantic interpretation of sentences that are inoperative in the perception of word lists. I will review the neuroimaging evidence supporting the role of the ATL in some form of combinatory processing; however, the neuropsychological data appear to support a nonsyntactic function for this region, but do support a role in combinatorial semantics.

The first study to employ the sentences > word lists approach, and with results representative of canonical findings in this regard, Mazoyer et al., (1993), found activation in bilateral ATL for sentences in the subjects' native language, whether coherent in a story, semantically anomalous, or with the content words replaced with pseudowords; but not for lists of words in the native language or sentences in a foreign language (fig. 4.1). In contrast, Broca's area activated for lists of words and stories in the native language, but not to semantically anomalous sentences or sentences with pseudowords (fig. 4.1). These results suggest that the ATL is involved whenever combinatory processing is required, but Broca's area does not. The essential finding of increased activation in the ATL to comprehension of sentences over word lists has been replicated several times (Humphries et al. 2005; Rogalsky & Hickok, 2009; Vandenberghe et al., 2002). Less consistent is whether the combinatory effect in the ATL is bilateral or unilateral, with some studies finding bilateral effects (Mazoyer et al., 1993; Rogalsky

& Hickok, 2009) and some studies finding left-lateralized effects (Humphries et al., 2005; Vandenberghe et al., 2002).

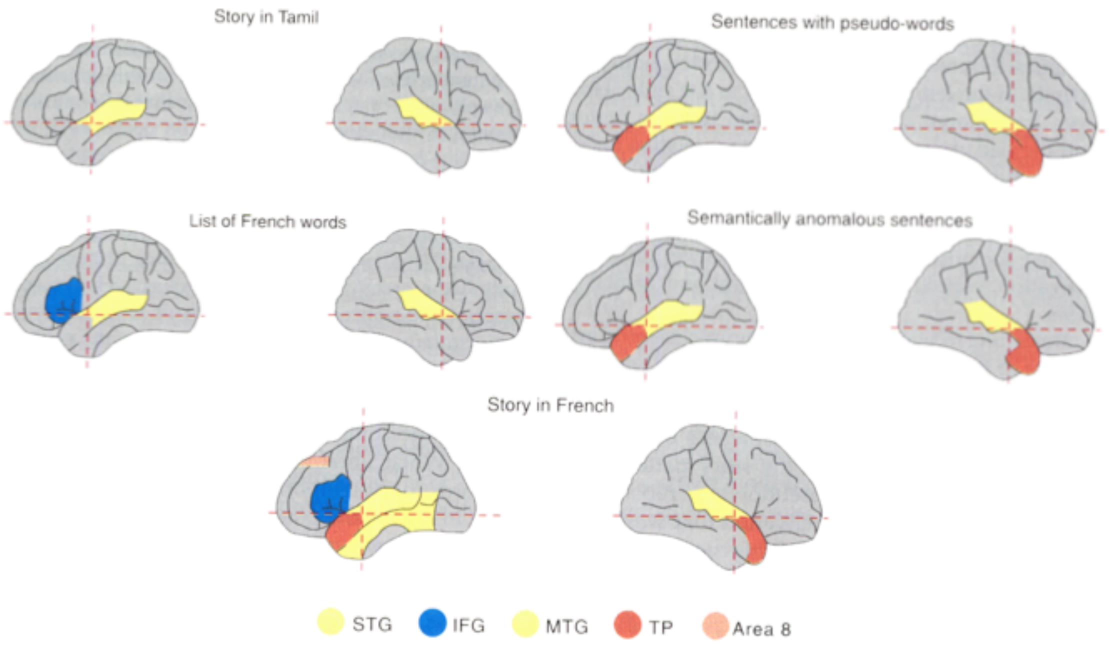


Figure 4.1 (adapted from Mazoyer et al., 1993). Activations obtained during processing of stories in a foreign language (top left), lists of words in the native language (middle left), sentences in the native language with content words replaced with pseudowords (top right), semantically anomalous sentences in the native language (middle right), and stories in the native language (bottom). The ATL, bilaterally (red), activates to sentences in the native language, while Broca's area (blue) activates to lists of words and stories in the native language, only.

In addition to increased activation to entire sentences versus word lists, the ATL is responsive to other manipulations of combinatory processing, suggestive of syntactic processing, but compatible with combinatorial semantics. Brennan et al. (2012) presented sentences to subjects in an fMRI study, and measured the activation to each word, correlating the signal with respect to the difficulty of integrating that word into the present syntactic structure, and showed a significant correlation between syntactic integration difficulty and activity of the left ATL. Bemis and Pylkkanen (2011), using MEG, investigated the processing of isolated adjective-noun combination, (e.g. "red boat"), to control conditions (e.g., "xkq boat"), finding increased activation in the ATL, bilaterally, to the second word (e.g., “boat”) for the combinatory condition. These effects were not due to multiple word presentations, as a similar two-word, but non-combinatory condition (e.g. “cup boat”), did not find increased activation relative to its control condition. Two other fMRI studies have also showed effects of syntactic structure in the ATL. Noppeney & Price (2004) obtained effects of syntactic repetition in the left ATL, wherein repetition of the same sentence constructions resulted in decreased activation in this region. Pallier et al. (2011) found increased activation with increased syntactic constituent size for phrases (e.g., constituent size = 12: *I believe that you should accept the proposal of your new associate* > constituent size = 6: *the mouse that eats our cheese two clients examine this nice couch* > constituent size = 2: *looking ahead important task who dies his dog few holes they write*) in both the left ATL and Broca’s area; however, they only obtained a significant effect in the ATL when they presented stimuli with real content words: when the content words were replaced with pseudowords, they did not obtain an effect in the ATL (although they still found effects in the *pars triangularis* of Broca’s area and the *pars orbitalis* of the IFG, in the vicinity of Broca’s area).

While these results suggest a potential role in syntactic operations, further examination reveals that the ATL is likely not involved in syntax itself. For example, as mentioned above, the Pallier et al. (2011) study only found activations correlating with syntactic constituent size in stimuli with real words, with semantic content, but not pseudowords, without semantic content. Other manipulations designed to tax syntactic operations do not always find activation in the ATL, suggesting an inconsistent response profile with respect to syntax. For instance, Rogalsky & Hickok (2009) presented subjects with sentences, asking them to selectively attend either to syntax or semantics; they obtained activation in subregions that preferred semantics, but no evidence of syntax-preferring subregions. In addition, studies of syntactic complexity or violations (e.g., Stromswold et al., 1996; Moro et al., 2001) do not always activate the ATL, although these negative findings do not constitute strong evidence against a role for syntactic operations in this region.

The neuropsychological literature is more compelling in speaking for a role of the ATL in sentence processing, but against a role specifically for syntax. Dronkers & Wilkins (2004) found that deficits in sentence comprehension in a large-scale study of patients with aphasia correlate primarily with damage to the ATL, strongly suggesting some role in sentence processing, whether syntactic, semantic or otherwise. Patients with atrophy to the ATL due to degenerative disease and language disorder, called primary progressive aphasia (semantic variant) or semantic dementia, typically show deficits in semantic processing (Hodges et al., 1992; Mesulam, 2013), but intact syntactic competence (Hodges et al., 1992; Mesulam, 2013, Wilson et al., 2014). These neuropsychological results, in conjunction with the canonical neuroimaging finding of increased activation to sentences over lists of words, suggests a role in combinatorial semantics, but not for syntactic structure building. Although our primary goal was to localize syntactic operations, a second goal of the current study was to provide further evidence to clarify the function of the ATL, be it combinatorial semantics or otherwise.

A complete neurolinguistic account of sentence comprehension will include such functions as combinatorial semantics, working memory, and cognitive control, among many others – as such, the ATL and Broca’s area are important components of the sentence-processing network. However, syntax is by many accounts the *core* linguistic component of sentence processing, and more broadly, language; we’d like to know something reasonable about the connection between syntax and brain. Given nonsyntactic roles for these regions, the search for syntax remains open, and to appropriately understand the neural instantiation of syntax, new approaches must be pursued. As such, we borrowed an experimental paradigm from the motor control literature, target perturbation, and used it to study syntax. This approach is legitimized from psycholinguistic research indicating that speakers use syntax in an online fashion during speech production, including updating their speech in response to syntactic variables (Fromkin et al., 1971; Ferreira & Swets, 2005). Before entering the details of our study, however, I would like to touch upon the extant neuroimaging literature on sentence production, as this has been less studied than sentence comprehension.

4.1.2 Sentence production and neuroimaging

As discussed throughout this dissertation, syntax has typically been studied through experimental paradigms manipulating syntactic variables such as complexity, distance, and violations in sentence *comprehension* (for more extensive reviews, see Friederici et al., 2011, and Rogalsky & Hickok, 2011). Fewer studies have studied overt sentence *production* or covert sentence *generation*; however, these studies demonstrate that there is substantial overlap of brain regions active for sentence processing during production as during comprehension (Del Prato & Pylkkanen, 2014; Haller et al., 2005; Menenti et al., 2011; Segaert et al., 2012; Golestani et al., 2006). Two of these studies compared sentence production to appropriate non-sentence control conditions, akin to the sentence vs. word list contrast used in sentence comprehension, finding activation in Broca's area, medial frontal areas (supplementary motor area, or SMA, and pre-SMA), and parietal cortex (Haller et al., 2005; Golestani et al., 2006), but notably not finding activation in the temporal lobe, either anterior or posterior, frequently reported for sentence comprehension (Friederici, 2011). Another set of studies has examined repetition effects (e.g., repetition suppression, or decreased activation for the repetition of a particular stimulus or process) for syntax, semantics, and words within language production and across production and comprehension (Menenti et al., 2011; 2012; Segaert et al., 2012; 2013). These studies reveal syntactic repetition effects primarily in the left hemisphere, including the posterior temporal lobe, inferior parietal lobe, medial frontal regions, Broca's area, and premotor cortex. These studies also revealed repetition effects for lexical items in the left ATL and posterior temporal lobe, as well as inferior frontal gyrus, and repetition effects for semantics in bilateral posterior temporal lobe. Finally, an MEG study by Del Prato & Pylkkanen (2014) showed that preparation to produce adjective-noun phrases (e.g., *red cup*) resulted in increased activation in the ATL relative to a control condition (e.g., *red, white*), while the combinatory effect did not generalize to quantifier-noun phrases (e.g., preparation to produce *two cups* did not activate this region more than preparation for *two, six*).

These effects suggest that particular components of the language network, including the ATL and Broca's area, are recruited during the production as well as the comprehension of sentences under particular conditions. However, a number of questions remain regarding the nature of sentence production and the brain. For one, what is the precise role of Broca's area during sentence production? Chapter 3 presented and extensively reviewed reasons why domain-general mechanisms, particularly working memory and/or cognitive control, account for activation during sentence processing. It is less clear if such functions operate during the production of sentences beyond simple articulatory coding. However, working memory broadly construed as consisting of retrieval, selection, and maintenance of lexical elements is plausibly involved in sentence production. For instance, to generate a sentence, a speaker needs to retrieve lexical items and integrate them into the utterance. The effects of lexical repetition effects in

Broca's area during production (Menenti et al., 2011; 2012) indicate that it supports lexical retrieval, whether construed as a component of working memory or not. Of course, additional psycholinguistic research would clarify the nature of linguistic variables in on-line speech production, and this would be helpful in clarifying the precise role of Broca's area in sentence production.

Secondly, the ATL is remarkably quiet in studies of sentence production when comparing production of sentences to nonsentence controls, with effects limited to lexical repetition (Menenti et al., 2011; 2012; Segaert et al., 2013) and phrasal combination (Del Prato & Pylkkanen, 2014). Given a role for abstract combinatorial semantics, one would expect activation for sentence production compared to control conditions that has been repeatedly found for sentence comprehension, but this result has not been reported (Haller et al., 2005; Golestani et al., 2006). There are several possibilities to explain this discrepancy. One is that the ATL is involved in combinatorial semantics only for comprehension; that is, in connecting external input to conceptual representations, rather than internal semantic processing, with some alternative explanation for the phrasal combination results in the ATL during production, such as lexical-level processing. A second possibility is that the region performs some other function than combinatorial semantics that is not tapped during sentence production, such as social cognition (Zahn et al., 2007; Ross & Olson, 2010). A third possibility is that the ATL is involved in combinatory semantics during sentence production, but that for some reason these effects were not detected with these neuroimaging methods. One goal of the present study was to further clarify the profile of activity in the anterior temporal lobe for the production of sentences and unstructured word lists, in particular, to determine whether we would obtain increased activity for sentences.

Finally, while these studies have provided valuable insight into the neural basis of sentence production, this literature is not as extensive as in sentence comprehension. In particular, there has not been an analog to syntactic violations, or experiments requiring subjects to alter or update the current syntactic structure, in sentence production. The main goal of the present study was to determine what the neural response to sentence production would be under demands of syntactic structure perturbation, requiring the subject to update the syntactic structure of his/her utterance, presumably requiring additional resources from brain regions involved in building syntactic structure. Our approach relies on the idea that subjects effectively use and update syntactic structure during sentence production, and I will review evidence in support of this idea below.

4.1.3 Online use of syntactic structure during sentence production

Since our goal was to induce increased demands on syntax during speech production, two critical assumptions our study are that subjects would create a syntactic plan in advance of production that could be perturbed by our manipulation, and that they could successfully update this syntactic plan mid-utterance. In essence, we asked subjects to begin producing a particular sentence, and required them to (i) plan the syntactic structure of their sentence in advance, (ii) notice and acknowledge the cue to update their sentence, (iii) update syntactic structure accordingly, and (iv) integrate the updated syntactic structure fluently into their ongoing utterances. If subjects did not plan the syntax of their sentences in advance, or were unable to truly integrate the updated syntactic plan mid-utterance, then our study would not be a valid investigation into syntactic operations. Evidence from psycholinguistic studies of sentence production forms the basis of our assumption of advance planning and on-line interactivity between syntax and speech production. Here, I will discuss two pieces of such evidence: first, data from speech errors indicating that syntactic structure forms a key component of speech planning during sentence production (Fromkin, 1971), and second, data from the online production of sentences indicating speech processing slowdowns on speech output due to upcoming syntactic violations (island violations), and the insertion of resumptive pronouns into island constructions (Ferreira & Swets, 2005).

4.1.4 Speech errors reflect syntactic planning during speech production

The fact that people speak in phrases and sentences rather than in random conglomerations of words or sounds makes obvious the fact that syntactic structure is imposed on our utterances. However, speech error data indicate that substantial syntactic structure is built in advance of speech production. These conclusions are supported by the fact that speech errors of substitution of words and phrasal constituents most always involve switches of the same syntactic category (Fromkin, 1971). For instance, consider the following lexical substitutions (from Fromkin, 1971):

(1) a **computer** in our own **laboratory** -> a **laboratory** in our own **computer**

(2) How come if you're a Scorpio you don't **read** – **wear** oriental spice?

In (1), two nouns are swapped for each other, indicating that the speech error was not a random misordering of words, but rather an error of lexical insertion into the phrasal structure. Similarly, in (2), a verb is replaced for a different verb. Now, consider the following phrasal substitutions:

(3) A **fall in pitch** occurs at the **end of a sentence** -> an **end of the sentence** occurs at the **fall in pitch.**

(4) He’s a **far better** man than anyone here -> he’s a **farther** man than anyone **better** here.

In (3), two complex noun phrases *fall in pitch* and *end of the sentence* are replaced for each other. In (4), *better* is displaced to the end of the sentence, and the adverb *far* is modified with an affix to become an adjective, which maintains the syntactic appropriateness of the noun phrase (i.e., not *he’s a far man than anyone better here*). The prevalence of speech errors such as these suggests that people build syntactic structure in advance of speech output, allowing the substitution of produced words in the same syntactic positions. However, the off-line analysis of speech errors gives little information about how and when interaction between syntax and speech production occurs. Research in psycholinguistics has shed some light on the on-line nature of speech production, mostly focusing on lexical access (Dell & O’Seaghdha, 1992; Levelt, 2001; Pickering & Branigan, 1998); however, research on syntactic structure itself during production has been much less studied. Such paucity likely has to do with the fact that experiments of single word production are much easier to control than studies of entire sentences or phrases. Regardless, at least one study has shed light on the interaction of syntactic structure and speech production, Ferreira & Swets (2005), examining production of sentences containing island violations and resumptive pronouns.

4.1.5 Syntactic islands, resumptive pronouns and speech production

Syntactic islands are illicit constructions, out of which Movement (reviewed in Chapters 2 & 3) is impossible (Ross, 1967). (5) is an example of a sentence containing an island violation, namely, a *subject island*:

(5) *We're afraid of things$_1$ that we don't know what [__$_1$] are.

When speakers accidentally produce sentences containing island violations, they will occasionally produce *resumptive pronouns*. Resumptive pronouns are anaphoric pronouns inserted into gap positions, referring to the moved constituent, of which the bold word in (6) is an example:

(6) *We're afraid of things$_1$ that we don't know what **[they$_1$]** are.

Interpretations of the function of resumptive pronouns (i.e., why they exist) vary, with one common-sense suggestion that they exist as a 'saving device', an attempt to repair an otherwise illicit construction (Boeckx & Lasnik, 2006). Regardless of the precise purpose of resumptive pronouns in English, their distribution is associated with syntactic islands, i.e., they are produced in island positions. Ferreira & Swets (2005) utilized this fact to study the incrementality of syntactic operations during sentence production (i.e., how much syntactic structure is planned in advance during speech production) by inducing subjects to produce sentences containing island violations with a priming technique and measuring their speech production times during island/resumptive sentences. When subjects produced sentences containing island violations and resumptive pronouns, they exhibited slowdowns (compared to an appropriate control condition with no island/resumptive) *prior* to production of the resumptive. The frequency of resumptive use increased and processing slowdown occurred earlier when subjects were not under time pressure, compared to when they had a deadline to produce their sentence, suggesting that the resumptive strategy was preferred when subjects had more time to think ahead. This result indicates that during sentence production, subjects build significant syntactic structure in advance, and this has ramifications on how quickly they produce speech and what they will produce next. In sum, there is good evidence to support advanced syntactic planning and online interactivity between syntax and speech production.

The present study aimed to measure the neural response to increased demands on syntax during speech production. Unlike resumptive pronouns, which are a natural case of on-line interaction between syntactic structure and speech production, the present study used an artificial perturbation paradigm to modulate syntactic demands, wherein the subject's target sentence occasionally changed mid-utterance, requiring the subject to update the chosen syntactic structure and integrate it into the corresponding phonological/articulatory plan.

4.1.6 The perturbation paradigm & the present study

The study reported here implements a perturbation paradigm, which has been used to study lower levels of motor control and speech production, similar to go/no-go experimental paradigms, which have been used to study response selection and action inhibition (Rubia et al., 2001; Simmonds et al., 2008; Swann et al., 2009). The perturbation paradigm in motor control studies involves the subject performing a movement with a sensory target, such as grasping an object at a particular location, or reaching from one point to another (Paulignan et al., 1991; Elliott et al., 1995; Izawa et al., 2008). On most trials, the subject's target and/or sensory feedback remain constant throughout duration of the movement. On a smaller proportion of trials, the subject's target or feedback is perturbed mid-movement, e.g., the visual target location is moved after onset of the reaching movement, or a force is applied to the subject's arm such that the movement ends up in a different location than expected. Experiments using perturbation in motor control have revealed fundamental properties of the motor control system, such as the presence of internal forward models, used for correcting movement trajectories before execution (Hickok et al., 2011; Shadmehr & Krakauer, 2008; Kawato, 1999), as well as the underlying neural bases of motor control and adaptation (Diedrichsen et al., 2005; Suminski et al., 2007). This technique has also been used in speech production (Houde & Jordan, 1998; Tourville et al., 2008; Golfinopoulos et al., 2011), revealing behavioral adaptation to perturbation of auditory and somatosensory feedback and the underlying neural bases of speech motor control.

We used the perturbation paradigm during sentence production in a novel design, in order to elucidate the neural networks involved in syntactic operations. I acknowledge the fact that our manipulation also involved non-syntactic mechanisms that will be conflated with syntactic operations, but our results, when interpreted with the appropriate caveats, provide new insight into the neural localization of syntax. Subjects were prompted with visual cues to produce sentences with a given syntactic structure: active (e.g., *Mary is hugging Charlie*) or passive (e.g., *Mary is being hugged by Charlie*). On a majority of trials (80%), there was no perturbation, and the subject produced the target sentence. On 20% of trials, mid-utterance, the target structure changed (i.e., active to passive; passive to active), requiring the subjects to update the planned sentence appropriately. What we expected during perturbation trials was for subjects to notice the changed demands, update the syntactic structure of the utterance, and continue producing the sentence. Syntactic structure-building operations were used in both control and perturbation trials, with the expectation that the updating of target sentence during perturbation trials increased the demand on regions involved in building syntactic structure, revealed through fMRI. To attempt to control for effects on non-syntactic mechanisms (e.g., visual processing, decision-making, lexical, phonological and articulatory processes), we included a control condition where subjects produced lists of words rather than sentences, using identical cues and the same task.

Our design allowed us to search for the networks involved in syntactic processing using a new perspective and technique, as well as investigate the response profile of Broca's area & the ATL, under different processing conditions than previously studied. For instance, our design allowed us to determine whether the sentences > word lists contrast showing activation in the ATL was upheld during sentence production, suggesting semantic processing regardless of comprehension or production, or whether this contrast only engages semantic processing as an interface to auditory comprehension. Likewise for Broca's area –we were able to determine whether demands on processing extend to the effects of syntactic perturbation on sentence production in our study. To test the functional response profile of these regions, we relied on the whole-brain analyses, as well as analyses in structural regions of interest (ROIs), based on cytoarchitectonics for Broca's area and its right hemisphere homolog, and coordinates in standard space (Talairach & Tournoux, 1988) in the left and right ATL obtained from a previous study exhibiting the sentences > lists effect in sentence comprehension (Rogalsky & Hickok, 2009).

4.2 Materials and methods

4.2.1 Subjects

21 right-handed, native speakers of English (age 19-33, 10 female) volunteered for participation. Subjects had normal or corrected-to-normal vision, no hearing impairment, and reported no history of neurological disorder. Subjects were paid $10 for participation in a one-hour behavioral training session. One subject was excluded from the fMRI portion of the experiment due to difficulty with the task during the behavioral session, resulting in 20 remaining subjects in the fMRI experiment. Subjects were paid $30 an hour for participation in the fMRI. Consent was acquired from each subject before participation and all procedures were approved by the Institutional Review Board of UC Irvine.

4.2.2 Stimuli

The stimuli for each trial consisted of a sequence of three cues, each of which contained the same basic template: simple line drawings of the actors engaged in the target sentence, the names of the actors in large font next to the drawings, the verb to be used in the sentence in the middle of the screen, and an arrow underneath the verb pointing to the right or the left (fig. 4.2). Identical cues with identical timing were used for both the sentences and lists conditions; only the subject's task changed between conditions. Twenty different verbs were used, all of them transitive, e.g. "follow", "hug", "punch", etc. Verbs varied from one to three syllables long, and were selected for a mix of articulatory complexity (see Appendix B to see a list of all verbs). Verbs were randomly distributed throughout the experimental runs. Four actors were used with the following names: Mary, Susan, Charlie, and Kevin. The first actor was always a different gender than the final actors, and actors were randomized distributed in different positions throughout the experimental runs. The line drawings of the actors were simple and strongly gender-typical to ease the subjects' recognition during the experiment. Three actors appeared on each cue: one actor on the left (START) and two on the right (END). The END actors were displayed one on top of the other. On the first cue, the PREP cue, the START actor was surrounded by a rectangular box, and the arrow, in black color, pointed from the START actors to in-between the END individuals, not biased toward either. The second cue, the GO cue, was identical to the first, but the box was removed from the image, serving as a "go" signal for the subject to begin articulating. The third cue, the FINAL cue, was identical to the second except that the arrow was blue and pointed to the target END individual for that trial. The PREP cue was presented for 500 ms to give subjects enough time to process the information and plan their utterances. The GO cue was displayed immediately after these 500 ms, and subjects were instructed to begin articulating in synchrony with this GO cue. The GO cue was presented for 300 ms, followed immediately by the FINAL cue, which remained on the screen for 1000 ms, followed by fixation until the next trial. During the behavioral training session, the subject would initiate the next trial whenever ready. During the fMRI study, the inter-trial-interval was fixed at 4200 ms, for a total trial duration of 6 s.

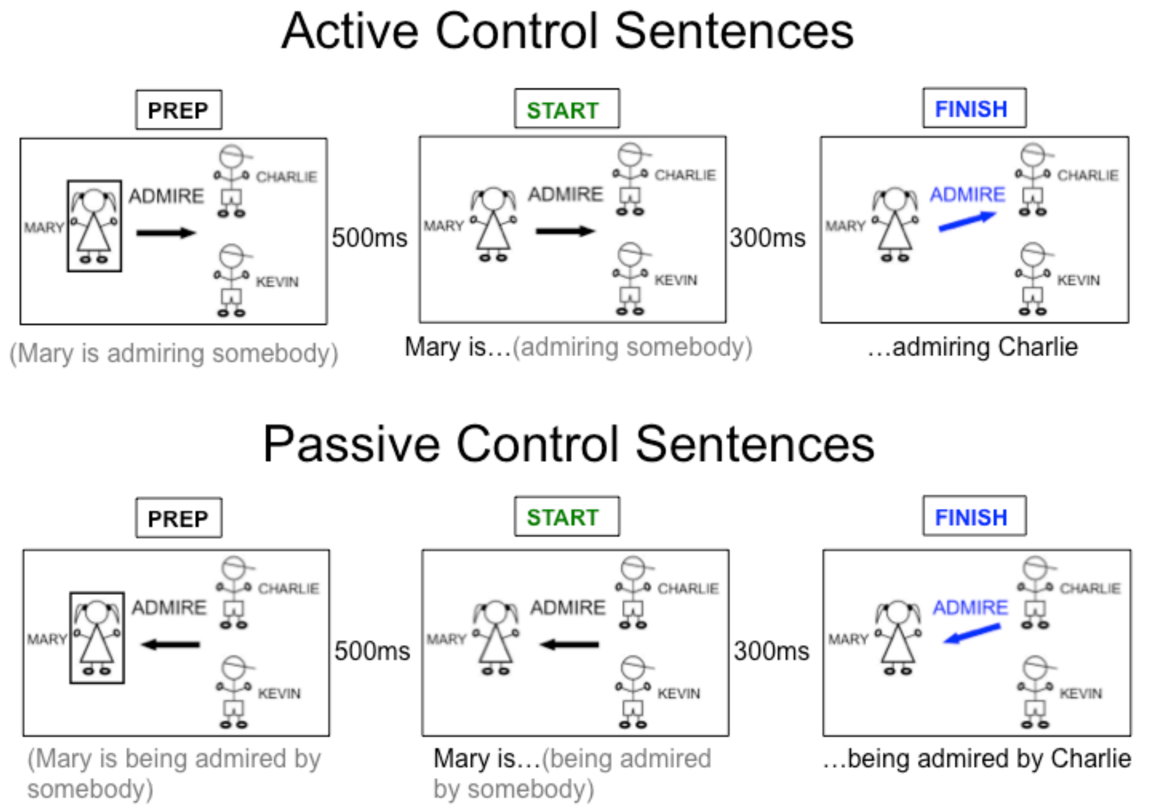


Figure 4.2. Schematized trial for control sentence trials, active (TOP) and passive (BOTTOM). The words under each picture indicate what the subject was able to plan (in grey) and what the subject produced, or began to produce (in black), when that cue was presented. LEFT: 'prep' cue, in which the subject prepared to begin producing the sentence with either active or passive construction. MIDDLE: 'start' cue, in which subject was cued to begin producing the incomplete sentence. RIGHT: 'finish' cue, in which the completing information was presented. On control trials, the subject's final structure was consistent with planning.

4.2.3 Task

Our experiment comprised a 2x2 design by task: the factors **STRUCTURE** (sentence, list) and **PERTURBATION** (control, switch). In the sentence condition, subjects were instructed to produce sentences, with either active or passive construction, with a fixed format detailed below. These two constructions comprised an additional factor within the sentence condition, based on the theoretical increased syntactic complexity of passive sentences compared to active sentences (Chomsky, 1965; 1981): **COMPLEXITY** (active, passive). Active sentences were cued with an arrow pointing away the first actor; passive sentences were cued with an arrow pointing toward the first actor (fig. 4.2). Active sentences were to be produced with this format: *(actor 1)* ***is*** *(verb)****ing*** *(actor 2),* e.g. *Mary is following Charlie*; passive sentences were to be produced with this format: *(actor 1)* ***is being*** *(verb)****ed by*** *(actor 2)*, e.g. *Mary is being followed by Charlie*. Subjects were instructed to use the progressive aspect morphology on every trial and not to deviate from this template. In the list condition, subjects were instructed to produce a list of words, based on the information presented on the cue. The subjects ignored the identity of the particular verb on the cue and did not use it in their lists. When the arrow pointed to the right, subjects produced a list with the following format: *(actor 1) word* ***right*** *arrow (actor 2)*, e.g., *Mary word right arrow Charlie*; when the arrow pointed to the left: *(actor 1) word* ***left*** *arrow (actor 2)*, e.g., *Mary word left arrow Charlie* (fig. 4.2). We chose the word *word* for the subjects to say in order to approximately control for the duration of planning and articulation that would take place for the word *is* in the sentence condition, as this was relevant to the timing of the switch trials and subjects' updating of their utterances (detailed below). Subjects were instructed in both conditions to make their utterances as fluidly and quickly as they would naturally speak.

The cues were presented such that the subjects did not know how to complete the sentence/list at the beginning of each trial. Only at the FINAL cue did subjects know which actor (top or bottom) would be the second actor in that trial. Subjects were instructed to begin their utterances at the GO cue, and incorporate the information on the FINAL cue to determine which actor's name they should produce. We set the GO cue to switch to the FINAL cue 300ms after onset to allow subjects enough time while speaking naturally to update their utterance without making mistakes on the switch trials. As an example, if the target sentence during sentence were "Mary is following Charlie", subjects were able to plan to speak "Mary is following …(actor 2)" at the GO cue, then 300 after they began speaking at the FINAL cue, they would be able to update their plan to include “Charlie”. Likewise for list; if the target list were “Mary word left arrow Charlie”, they would be able to plan “Mary word left arrow (actor 2)” at the GO cue, and update as necessary at the FINAL cue.

Control trials occurred exactly as described above; switch trials involved not only updating actor 2, but also switching the orientation of the arrow (fig. 4.3). On such trials, during sentence, the subjects needed to switch their target sentence from active to passive or vice versa, e.g. *Mary is following (actor 2)* ➔ *Mary is* ***being followed by Charlie***. During list, subjects needed to switch whether they said *right arrow* or *left arrow*, e.g. *Mary word left arrow (actor 2)* ➔ *Mary word* ***right arrow Charlie***. Control and switch trials were presented at a 4/1 ratio and in random order within each run, such that subjects could not predict what the next trial would be. We utilized this ratio because this approximate ratio was used in previous studies of target perturbation and fMRI (3/1 ratio used by Tourville et al., 2008), and a smaller ratio of control to switch trials might have resulted in subjects anticipating switch trials and not committing to a syntactic plan on every trial in order to avoid errors.

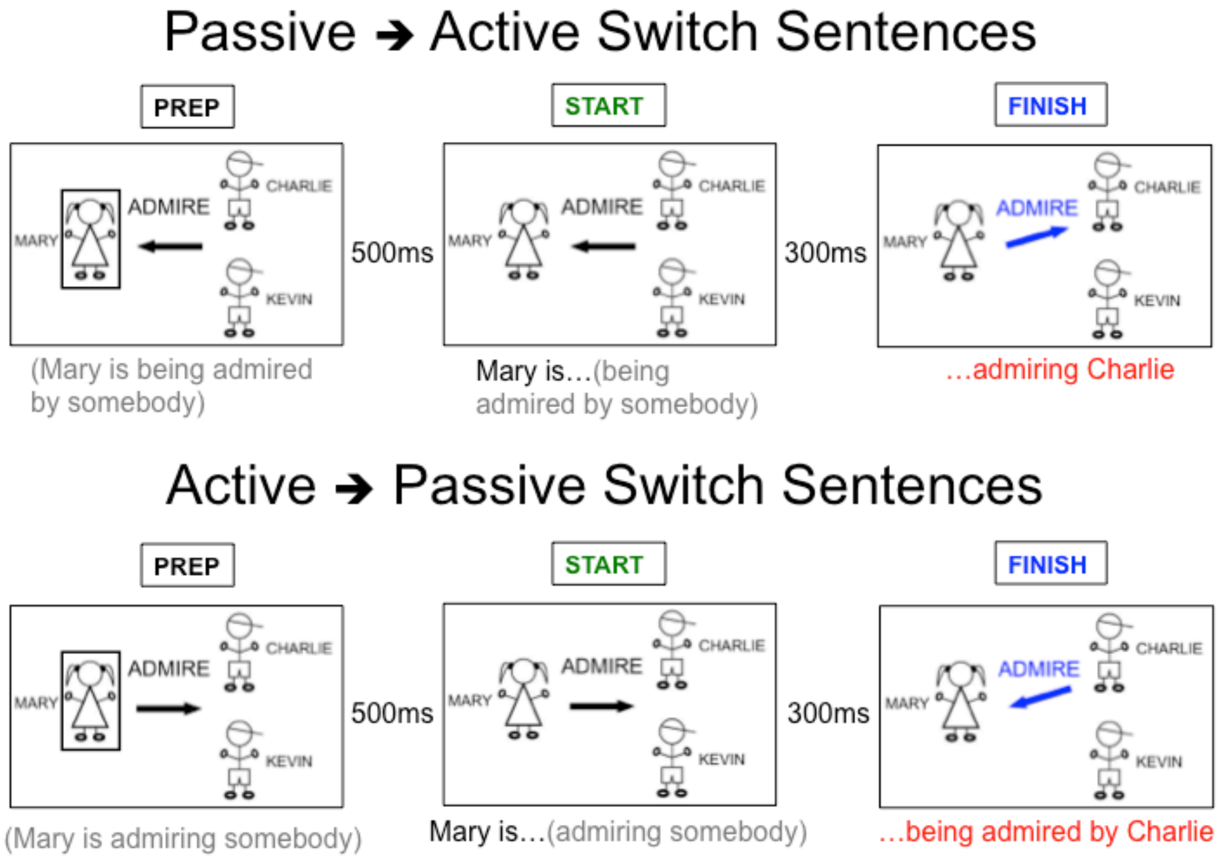


Figure 4.3. Schematized trial for switch (perturbation) sentence trials, passive to active (TOP) and active to passive (BOTTOM). The words under each picture indicate what the subject was able to plan (in grey) and what the subject produced, or began to produce (in black), and what the subject produced after updating the sentence construction (in red) when that cue was presented. LEFT: 'prep' cue, in which subject prepared to begin producing the sentence with either active or passive construction. MIDDLE: 'start' cue, in which subject was cued to begin producing the incomplete sentence. RIGHT: 'finish' cue, in which the completing information was presented. On switch trials, the subject would have to change from one structure to another.

The sentence and list conditions were presented in separate runs to avoid task-switching effects aside from the PERTURBATION manipulation. To control for spatial orientation of the cues, we presented subjects with cues that flowed from left to right (as depicted in figs. 4.2 and 4.3) and cues that flowed from the opposite direction, right to left. Subjects always received two runs from either the sentence or list condition in a row with both cue orientations (order counterbalanced across subjects), and we collapsed all analyses across the two orientations.

4.2.4 Behavioral training session

Before running the experiment in the fMRI scanner, we familiarized subjects on the task in a behavioral training session. In the training session, the task was explained to the subjects, including a demonstration by the experimenter on several trials. Then, subjects were asked to perform the task themselves. In the first several trials, the experimenter remained present in order to give feedback and instruction, and when the subject appeared to grasp the task, the experimenter left the room and the subject proceeded in a self-paced fashion. Subjects performed both tasks with both orientations for a total of four experimental runs, consisting of 50 trials apiece, for a total of 100 trials in the sentence condition and 100 trials in the list condition. The subjects' utterances were recorded and their performance was analyzed. A subject's response was considered an error if they produced the incorrect sentence construction (e.g., active instead of passive) or produced right instead of left, or if they made a speech error during the trial (e.g., produced the wrong speech sound, extensive delays, etc.). Errors of substituting the names of actors (e.g., *Mary* instead of *Susan*) or substituting one verb for another (e.g., *push* instead of *punch*) were not counted as errors, unless the subject also made a speech error. We were only able to collect and analyze behavioral data from 15 out of 20 subjects. Subjects participated in the fMRI experiment after completing the behavioral session, either the same day or on a subsequent day, within a week after the behavioral session.

4.2.5 fMRI experiment

Before scanning, subjects were briefly re-familiarized with the task by performing a few trials in each condition. Subjects were instructed to produce their utterances out loud in the scanner, but quietly. Subjects received 12 total experimental runs during the experiment (six sentence, six list, counterbalanced by orientation). During the experiment, a fixation cross was displayed on a screen in-between presentation of the cues. Stimuli were delivered with Matlab software (Mathworks, Inc., USA), utilizing Psychtoolbox (Brainard, 1997; Kleiner et al., 2007). Subjects were given ear covers and foam earplugs to attenuate scanner noise. The experiment consisted of the 12 experimental runs followed by a high-resolution anatomical scan. Within experimental runs, 40 control trials and 10 switch trials were presented to the subject in random order, with no explicit rest trials. Presentation order of sentence and list runs was counterbalanced along with cue orientation across subjects. Active/passive constructions were presented equally as well as left/right arrow lists. The high-resolution anatomical image was collected last. The scanning session lasted about one hour and fifteen minutes in total.

4.2.6 fMRI data collection and preprocessing

MR images were obtained in a Philips Achieva 3T (Philips Medical Systems, Andover, MA) fitted with an eight-channel RF receiver head coil at the high field scanning facility at UC Irvine. We first collected a total of 1896 T2*-weighted EPI volumes over 12 runs using Fast Echo EPI in ascending order (TR=2s, TE=25ms, flip angle = 90◦, in-plane resolution = 1.95mm × 1.95mm, slice thickness = 3mm with 0.5mm gap). The first four volumes of each run were collected before stimulus presentation and discarded to control for T1 saturation effects. After the functional scans, a high-resolution T1-weighted anatomical image was acquired in the axial plane (TR=8ms, TE=3.7ms, flip angle=8◦, size=1mm isotropic).

Slice-timing correction, motion correction, and spatial smoothing were performed using AFNI software (http://afni.nimh.nih.gov/afni). Motion correction was achieved by using a 6-

parameter rigid-body transformation, with each functional volume in a run first aligned to a single volume in that run. Functional volumes were aligned to the anatomical image, and subsequently aligned to Talairach space (Talairach and Tournoux, 1988). Functional images were resampled to 2.5mm isotropic voxels, and spatially smoothed using a Gaussian kernel of 6mm FWHM. Finally, functional images were rescaled to reflect percent signal change from the mean signal during each run.

4.2.7 Whole-brain analyses

First-level analyses were performed on each individual subject's data using AFNI's 3dDeconvolve function. The regression analysis was performed to find parameter estimates that best explained variability in the data. Each predictor variable representing the time course of activity associated with the task was entered into a deconvolution analysis that estimated parameters best representing the timecourse of the hemodynamic response function in percent signal change values. Timecourse estimates were modeled beginning with the onset of the GO cue, i.e., when the subject began producing the sentence. The following eight regressors of interest were used in the experimental analysis: sentence active, sentence passive, list left, list right, sentence switch: active to passive, sentence switch: passive to active, list switch: left to right, and list switch right to left. The six motion parameters were included as regressors of no interest. Second-level group analyses were then performed, entering the values from the experimental contrasts from each subject and condition into a mixed-effects analysis with subjects as random variables, using AFNI's 3dMEMA function, for the following contrasts: sentence vs. list (**STRUCTURE**), active vs. passive (**COMPLEXITY**), and switch vs. control (**PERTURBATION**). Because we were particularly interested in switch effects preferentially for the sentence condition, we examined the simple effects of PERTURBATION for sentence and list separately, and ran an interaction analysis of STRUCTURE and PERTURBATION.

4.2.8 ROI analyses

Given the extensive literature documenting a relationship between Broca's area, the ATL and sentence processing, we performed ROI analyses on these regions. As such, we extracted percent signal change values within structural ROIs for these regions and the right hemisphere homolog of Broca's area, and ran statistical analyses. For Broca's area and its right hemisphere homolog, we used templates in Talairach space for BA44 and BA45 provided by AFNI based on the cytoarchitectonic probability maps of Amunts et al. (1999). For the ATL, the relevant functional regions of interest do not align well to probability maps based on cytoarchitectonics. As such, we constructed left and right ATL ROIs based on coordinates reported in the neuroimaging literature: we obtained the center of mass coordinates reported by Rogalsky & Hickok (2009) for the sentence > list contrast in the left and right ATL, and created spheres with radius 7.5 mm around the coordinates. We averaged across all voxels within each ROI and collapsed our analyses across construction in the sentence conditions and direction in the list conditions, resulting in 2x2 ANOVAs for each ROI (STRUCTURE x PERTURBATION).

4.3 Results

4.3.1 Behavioral performance

The behavioral performance of the 15 subjects for whom we collected data is displayed in fig. 4.4. For non-switch control trials, subjects performed near ceiling for the sentence and list conditions. Subjects performed significantly worse than control during switch trials in the sentence condition, but no differently than control during switch trials in the list condition. Even though subjects' performance dropped during switch sentence trials, their performance was still above 80%, indicating that they could successfully perform the task.

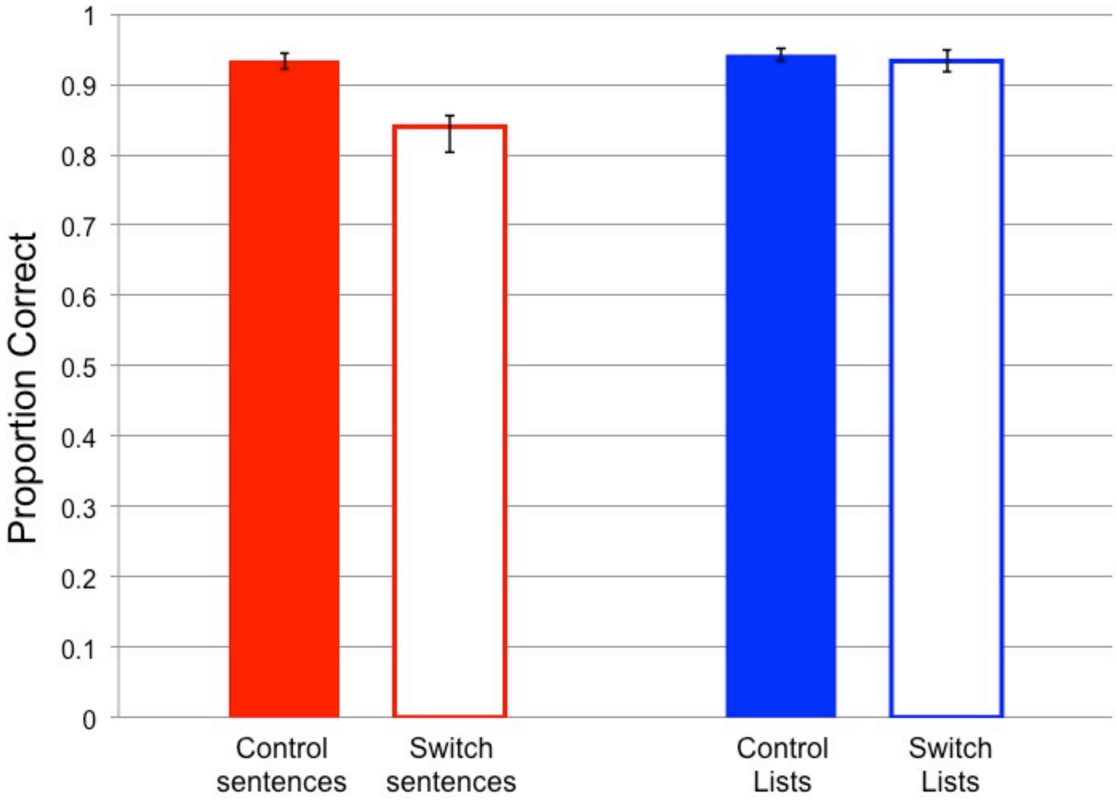


Figure 4.4. Performance by 15 subjects in the behavioral pre-scan training session. Data are collapsed across orientation of cue, and collapsed across constructions in the sentence conditions and right/left arrow in the list conditions. Error bars indicate standard error of the mean.

4.3.2 Whole-brain fMRI analyses

The whole-brain contrasts of STRUCTURE and COMPLEXITY did not reveal activation in the ATL or Broca's area, as previously reported in the literature for comprehension, but did reveal effects in sensory-motor regions. The effect of STRUCTURE (sentences > lists) revealed increased activation for sentences in left visual cortex, left posterior STS/MTG, right precentral gyrus, right postcentral gyrus, bilateral middle frontal gyrus, and left caudate (fig. 4.5, left). The effect of syntactic COMPLEXITY (passive > active sentences) did revealed one cluster in the right postcentral gyrus (fig. 4.5, right).

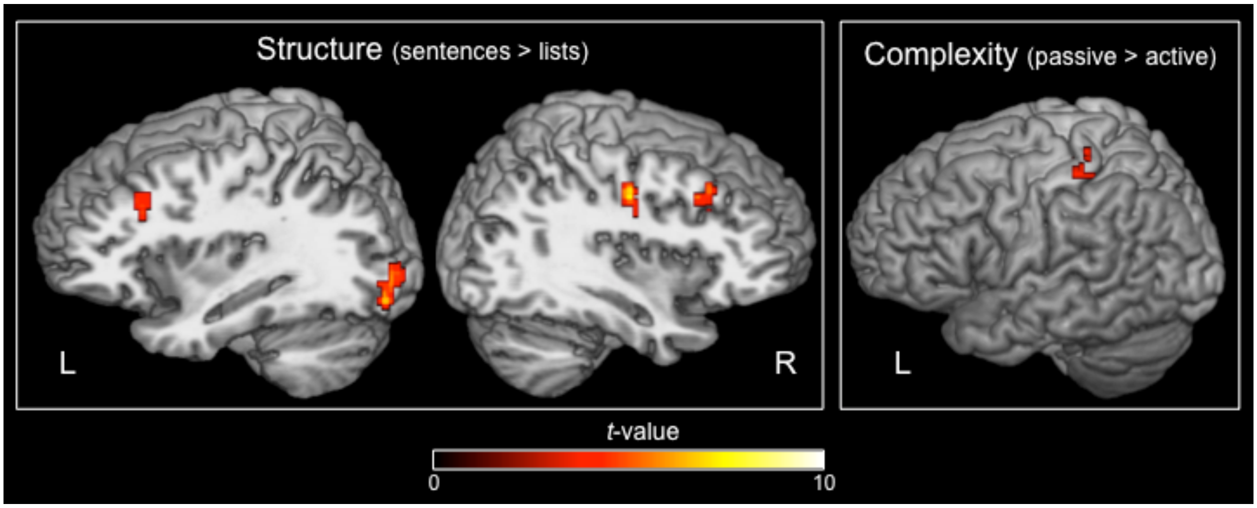


Figure 4.5. LEFT: Activations for the STRUCTURE contrast (sentences > word lists). RIGHT: Activations for the COMPLEXITY contrast (passive > active). $N = 20$. Activations for both contrasts are cluster-corrected for multiple comparisons at $p < 0.05$ (one-tailed).

The effect of PERTURBATION in the sentence condition (sentence switch > sentence control), which we assumed would tax neural networks involved in syntax, revealed increased activation during the switch condition in a network including areas typically found for manipulations of response selection/inhibition (Simmonds et al., 2008) and motor control (Tourville et al., 2008; Diedrichsen et al., 2005) (fig. 4.6); particularly notable was strong activation in the right IFG/anterior insula that has been shown to be specifically involved in “stopping”, or the cancellation of a planned response (Aron et al., 2003; Swann et al., 2009). Activations for this contrast included the supplementary motor area (SMA), pre-SMA, basal ganglia (right caudate nucleus), left inferior parietal cortex, right STS, and right IFG/MFG.

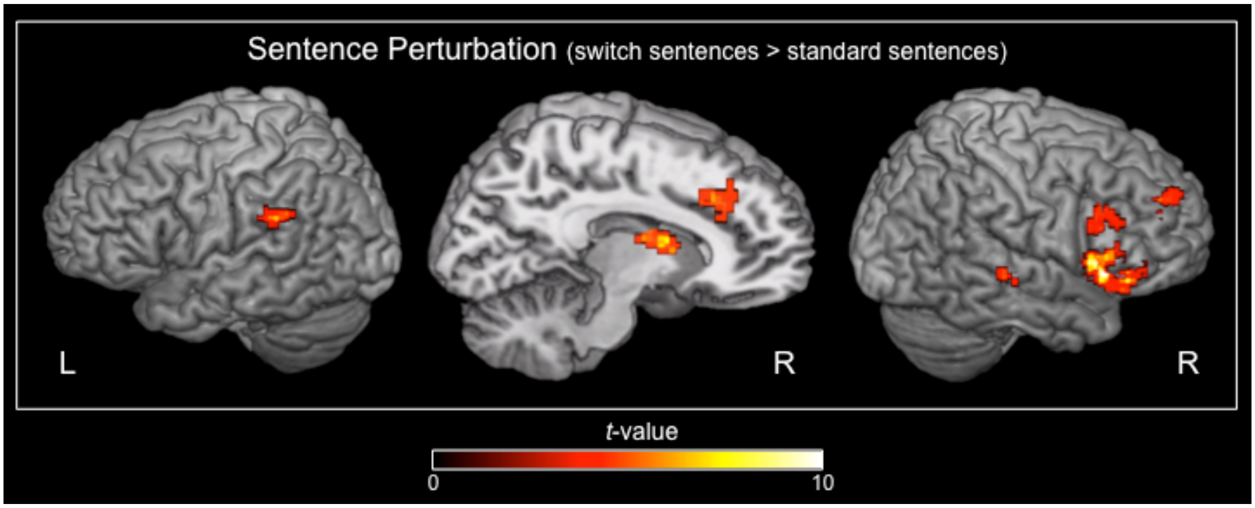


Figure 4.6. Activations for the sentence PERTURBATION contrast (switch sentences > control sentences). $N = 20$. Activations cluster-corrected for multiple comparisons at $p < 0.05$ (one-tailed).

The effect of PERTURBATION in the list condition (list switch > list control) revealed effects in the SMA and cerebellum (fig. 4.7). Notably, while the effects for PERTURBATION in the list condition were similar to activations for PERTURBATION in the sentence condition in medial frontal regions (SMA) thought to be involved in decision-making and response preparation, PERTURBATION in the list condition did not reveal effects in the right IFG “stopping” network or the caudate nucleus. The interaction contrast of PERTURBATION with STRUCTURE revealed, at a reduced threshold, that there was increased activation for PERTURBATION in the sentence condition compared to the list condition in the right IFG, the thalamus, left inferior parietal cortex, and the right posterior STS (fig. 4.8).

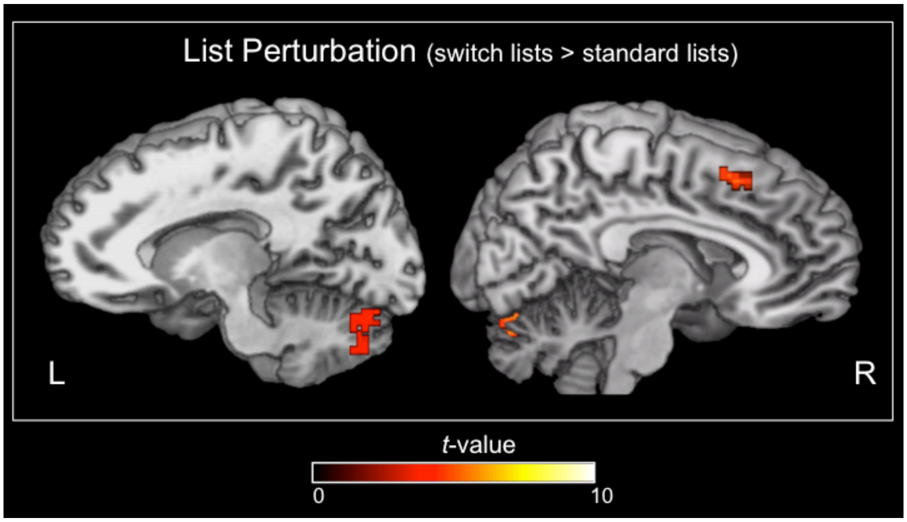


Figure 4.7. Activations for the list PERTURBATION contrast (switch lists > control lists). *N* = 20. Activations cluster-corrected for multiple comparisons at $p < 0.05$ (one-tailed).

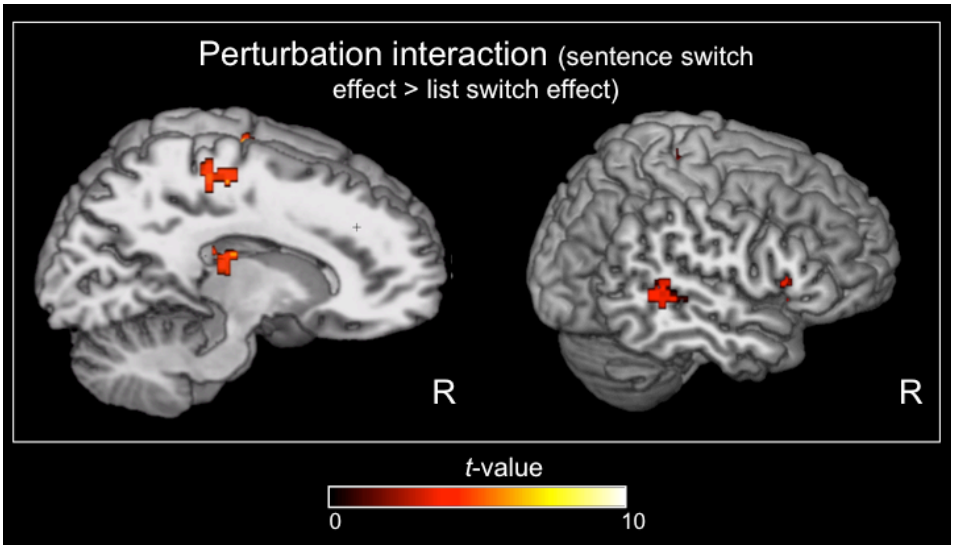


Figure 4.8. Activations for the PERTURBATION interaction (sentence switch effect > list switch effect). *N* = 20. Activations are displayed at an uncorrected threshold, $p < 0.005$ (one-tailed), with a minimum cluster extent of 312.5 mm^3 (20 voxels).

Because the behavioral data indicated that subjects made more speech errors due to perturbation in the sentence condition than the list condition, and any effects of syntax are conflated with difficulties in speech production, we decided to run an analysis on PERTURBATION in the sentence condition from the 15 subjects for whom we collected behavioral data and analyze the performance during the sentence switch condition as a covariate. The results of this analysis, at a reduced threshold, indicated that better speech performance on the behavioral task positively correlated with activations similar to those found in the syntactic PERTURBATION contrast, including a right-lateralized network including anterior caudate, cingulate gyrus, posterior middle temporal areas, some subcortical activation, and medial anterior temporal areas (Table 4.1), but not did not account for the right inferior frontal activation, the activation in the middle caudate body, right thalamus, or anterior medial frontal activation found in the contrast. Therefore, it seems as though there were effects of the syntactic PERTURBATION manipulation not directly reducible to the subjects' speech errors.

Table 4.1

Region	Hemisphere	x	y	z	Cluster Size (mm3)
Positive effect of covariate					
Cingulate gyrus	Right	20	-24	31	1688
Posterior middle temporal gyrus	Right	45	-48	4	875
Inferior parietal lobule	Right	44	-30	44	531
Anterior caudate	Left/Right	3	5	12	422
Anterior middle temporal gyrus	Right	45	-6	-19	313
Parahippocampal gyrus	Right	35	-12	-23	297
Cerebellum	Right	33	-70	-31	188
Middle frontal gyrus	Right	25	38	-3	172
Posterior middle temporal gyrus	Right	46	-69	6	156
Negative effect of covariate					
Cerebellar vermis	Right	5	-40	-35	156
Anterior cingulate	Left/Right	1	26	14	156
Precentral gyrus	Left	-29	-7	35	156

n = 15. Individual voxel threshold $p < 0.01$ (two-tailed), cluster size threshold 156 mm^3 (10 voxels).

4.3.3 ROI analyses

For all ROI analyses, we averaged effects across active and passive construction, as well as both directions in the list condition, as we wanted to focus on effects of PERTURBATION (switch vs. control) and STRUCTURE (sentences vs. lists), based on our expectations from the literature. Activations for each condition in left IFG ROIs are displayed in fig. 4.9. In left BA44, there were no significant effects of STRUCTURE, $F(1,19) = 1.839$, $p = .191$, or PERTURBATION, $F(1,19) = 1.179$, $p = .291$, and no significant interaction, $F(1,19) = .065$, $p = .802$. In left BA45, there were no significant effects of STRUCTURE, $F(1,19) = .001$, $p = .979$, or PERTURBATION, $F(1,19) = .272$, $p = .608$, and no significant interaction, $F(1,19) = 1.691$, $p = .209$. Activations for each condition in right IFG ROIs are displayed in fig. 4.10. In right BA44, there was a significant effect of STRUCTURE, $F(1,19) = 7.707$, $p = .012$, with less deactivation in the list conditions compared to the sentences, and no effect of PERTURBATION, $F(1,19) = .151$, $p = .702$, or the interaction, $F(1,19) = .276$, $p = .605$. In right BA45, there was a significant effect of STRUCTURE, $F(1,19) = 13.615$, $p = .002$, with less deactivation in the list conditions compared to the sentences, and no effect of PERTURBATION, $F(1,19) = .034$, $p = .855$, or the interaction, $F(1,19) = 1.142$, $p = .299$.

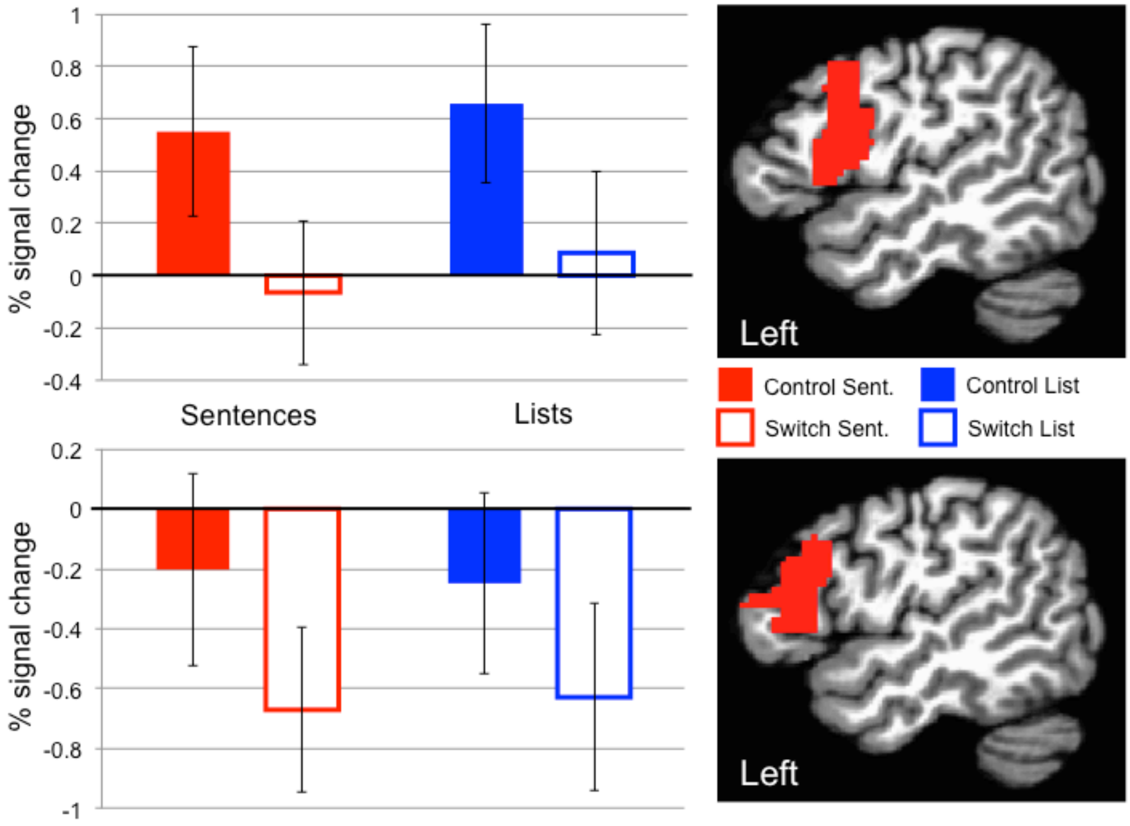


Figure 4.9. ROI analyses for the left IFG. TOP: left BA44, no significant effects of PERTURBATION, STRUCTURE, or the interaction. BOTTOM: left BA45, no significant effects of PERTURBATION, STRUCTURE, or the interaction. Error bars indicate standard error of the mean.

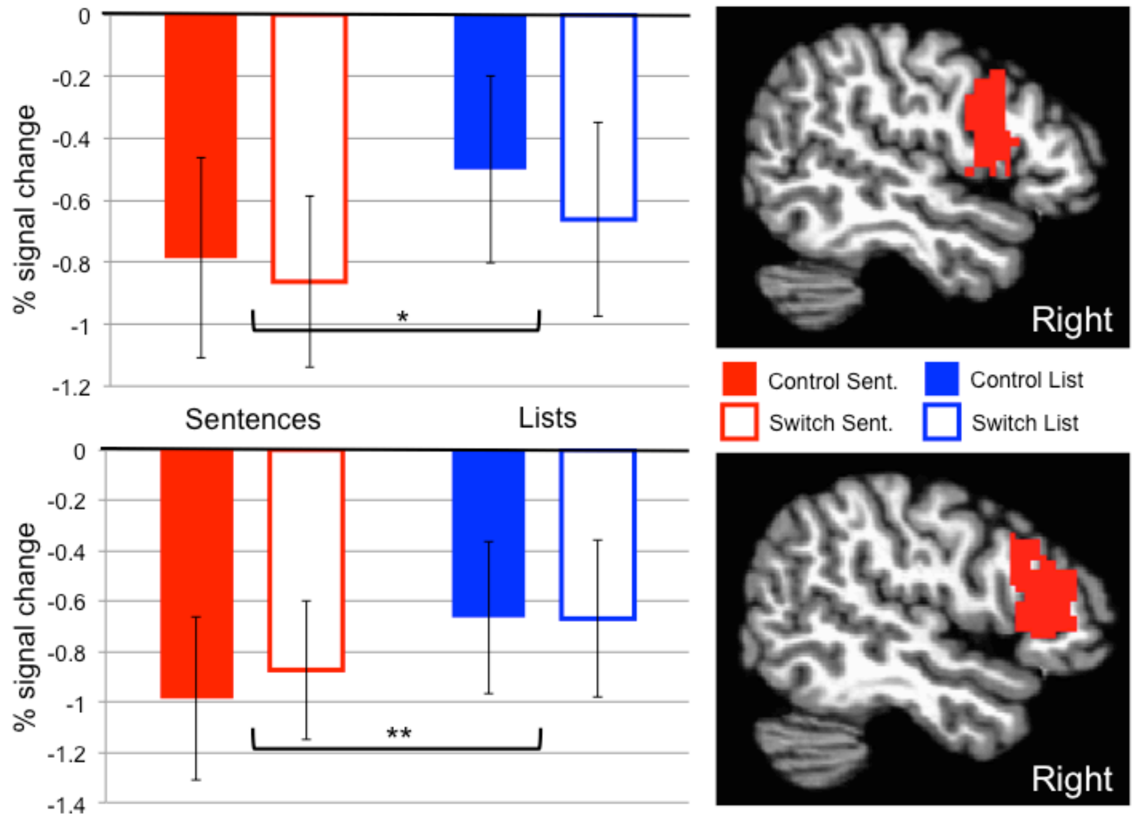


Figure 4.10. ROI analyses for the right IFG. TOP: right BA44, a significant effect of STRUCTURE, with no effect for PERTURBATION or the interaction. BOTTOM: right BA45, a significant effect of STRUCTURE, with no effect for PERTURBATION or the interaction. Error bars indicate standard error of the mean.

Activation for each condition in left and right ATL ROIs are displayed in fig. 4.11. In the left ATL, there was a significant effect of STRUCTURE, $F(1,19) = 6.918$, $p = .016$, with no effect of PERTURBATION, $F(1,19) = .887$, $p = .358$ or the interaction, $F(1,19) = 2.964$, $p = .101$. While the interaction was not significant, it is clear that the effect of STRUCTURE is being driven by increased activation in the control sentences. In the right ATL, there was a significant effect of STRUCTURE, $F(1,19) = 7.753$, $p = .012$, with no effect of PERTURBATION, $F(1,19) = .011$, $p = .916$ or the interaction, $F(1,19) = .471$, $p = .501$. Unlike the left ATL, the effect of STRUCTURE is clear by noting increased activation for both sentence conditions relative to word lists.

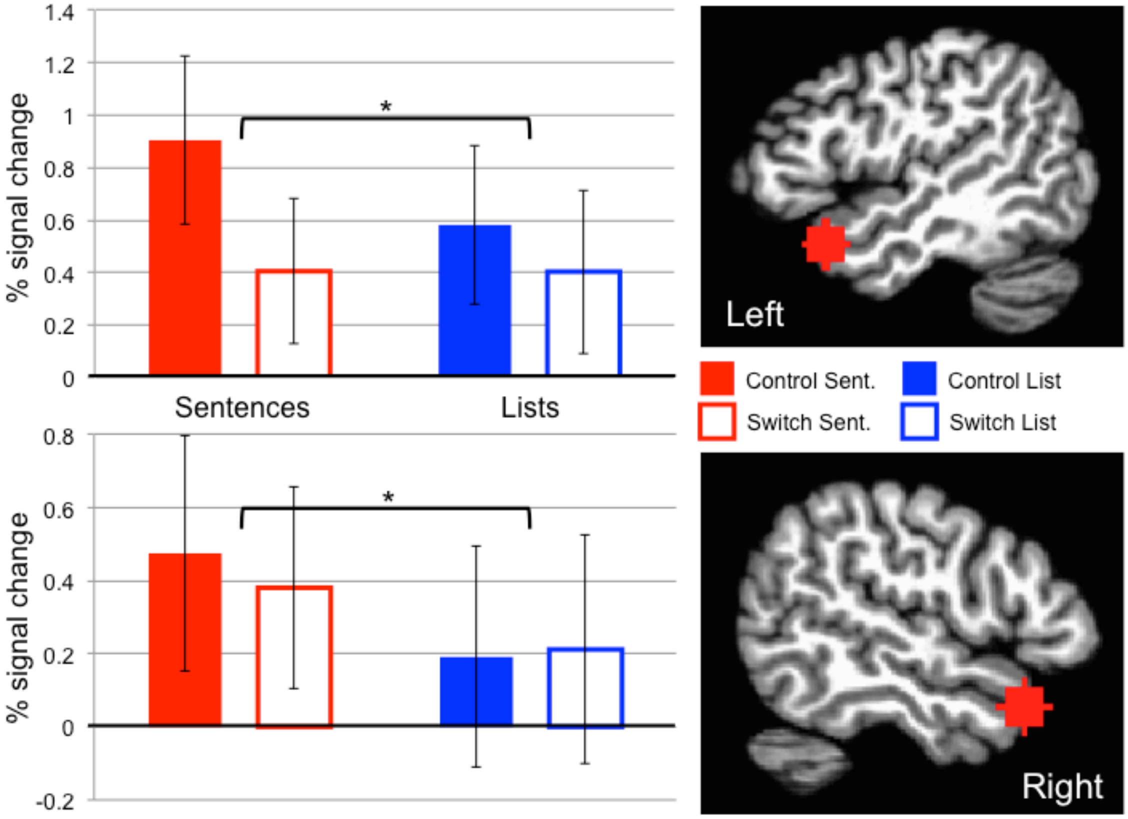


Figure 4.11. ROI analyses for the left and right ATL ROIs. TOP: left ATL, a significant effect of STRUCTURE, with no effect for PERTURBATION or the interaction. BOTTOM: right ATL, a significant effect of STRUCTURE, with no effect for PERTURBATION or the interaction. Error bars indicate standard error of the mean.

4.4 Discussion

In the present study, we implemented a novel experimental paradigm in the effort to understand the neural bases of sentence processing: a syntactic ‘perturbation’ paradigm, in which subjects were required to produce sentences according to a fixed syntactic structure, and update their syntactic ‘target’ mid-utterance on a smaller proportion of trials. Our primary goal was to elucidate the neural networks involved in syntactic structure building, which have been previously studies using various manipulations of syntactic complexity and syntactic violations, distance manipulations, or comparing activation of sentences to unstructured word lists. In addition, we sought to characterize the response profile of brain regions previously implicated in syntax- and sentence-level processing to our manipulation; namely, the left IFG (Broca's area), the right IFG, and the left and right ATL. The syntactic perturbation manipulation resulted in activation in a network of regions involved in response selection, action inhibition, and motor control; our control condition, perturbation of non-syntactic word lists, resulted in a similar network, with some important differences. Notably, the right IFG exhibited significant effects of syntactic perturbation; however, given this region's involvement in non-syntactic processes of response inhibition, it likely plays a non-syntactic role in sentence production. Rather, the results suggest differences between sentences and lists in terms of their interaction with the speech production system (discussed below). The response profile of Broca's area did not show substantial effects of syntactic perturbation, and a similar response profile for both sentences and word lists, consistent with a domain-general function for sentence processing, as discussed in Chapter 3. The left ATL replicated effects of sentences > word lists found elsewhere in the literature, consistent with a role in semantic processing, but did not show increased activity during syntactic perturbation (if anything, there was an effect of *decreased* activity for syntactic perturbation), speaking against a role in syntactic structure-building. The right ATL showed similar effects for sentences and word lists, suggesting a domain-general function not specific to combinatory semantics. Our results suggest that syntactic structure building may rely on similar networks to motor control, consistent with the role of syntax as a generative procedure, rather than Broca's area or the ATL; however, our results are tentative, given the novelty of our experimental paradigm.

4.4.1 Syntactic perturbation reveals a network for response selection, action inhibition, and motor control

While the whole-brain contrasts of STRUCTURE (sentences > lists) and COMPLEXITY (passive sentences > active sentences) did not reveal effects beyond low-level sensory-motor networks, the perturbation manipulation in the sentence condition activated medial frontal areas (SMA, pre-SMA), basal ganglia (right caudate nucleus), left inferior parietal cortex, right posterior STS, and right FG; regions that have been reported in studies of perturbation and motor control in other domains (Tourville et al., 2008; Diedrichsen et al., 2005; Suminski et al., 2007), along with studies of response selection/action inhibition implementing go/no-go designs (Simmonds et el., 2008). While the list perturbation condition also activated the medial frontal regions and the cerebellum, it did not reveal activation in the right IFG, the basal ganglia, or the right posterior STS. In addition, the interaction contrast, at a reduced threshold, indicated that sentence perturbation activated the right IFG, thalamus, and right posterior STS significantly more so than the list condition.

Given the similarity of these activations to effects found for other domains of motor control, there are at least two logical possibilities to account for such activations: (i) the activations reflect syntactic operations, which reside in similar neural territory as some component of motor control, or (ii) the activations merely reflect increased demands on lower-level motor control, and do not reveal anything specific to syntax. Possibility (ii) is a salient possibility, particularly given the behavioral results showing that subjects made more errors in the sentence condition, and likely struggled more to control their speech output in this condition. However, the analysis of behavioral covariates on performance during the behavioral task in the sentence switch condition revealed a positive correlation between better performance and increased activation in a similar, but different, right-lateralized motor control network, suggesting that the activations due to syntactic perturbation cannot be accounted for purely by increased reliance on speech motor control. Possibility (i) is an interesting one, when one considers that motor control and syntax may share some fundamental properties, including structure/sequence building and cost minimization. In motor control, the goal is to select a motor sequence while minimizing computational cost (Hickok et al., 2011, Shadmehr & Krakauer, 2008). In the minimalist program (Chomsky, 1995; 1999), syntax generates syntactic structures while minimizing computational cost. It may be that subcortical networks, including the basal ganglia and thalamus, are important in structure/sequence building and cost minimization. This proposal bears some similarity to proposals of previous authors, who have highlighted the computational similarity of sequencing in motor control to syntactic operations (Lieberman, 2002; Bornkessel-Schlesewsky & Schlesewsky, 2013). Previous neuroimaging studies of syntax have also shown activations in subcortical structures, including the basal ganglia and thalamus (Friederici et al., 2003; Humphries et al., 2005; Bahlmann et al., 2008; Moro et al., 2001), and neuropsychological data suggest some association of subcortical structures with syntactic processing (Kotz et al., 2003; Ullman et al., 1997; but see Grossman et al., 2002).

However, there is insufficient evidence to draw any firm conclusions. Given that subjects made more errors and generally had a more difficult time adapting to switches in the sentence conditions, it is difficult to reject the simple hypothesis that these activations reflect lower-level processes relied more heavily upon due to syntactic perturbation, the analysis of behavioral covariates or speech errors notwithstanding. More research with appropriate controls for low-level motor control will be needed to determine whether the analogy of syntax to motor control has any traction.

4.4.2 Syntactic perturbation and Broca's area

Our secondary goal was to further characterize the functional profile of activity in extant ROIs for syntactic processing: Broca's area and the ATL. Broca's area showed no evidence of increased activation for syntactic perturbation, sentence complexity, or structure. These results, along with considerations more extensively discussed in Chapters 2 & 3, strongly indicate that Broca's area is unlikely to be involved in syntactic structure building. The right hemisphere homolog of Broca's area, the right IFG, did show substantial effects of syntactic perturbation in the whole-brain analyses, and effects of structure in the ROI analyses however. However, these effects indicate a nonsyntactic function of the right IFG (particularly given that the effect of structure was such that there was increased activity in the *list* condition).

4.4.3 The right IFG, syntactic perturbation, and action inhibition

In the right IFG, we obtained effects of PERTURBATION in the sentence condition in the whole-brain analyses. Interestingly, while the ROI analyses hint at some effects of PERTURBATION in the list condition, these effects were not significant in the whole-brain analyses, and the interaction analysis (at a reduced threshold) indicated a stronger effect of PERTURBATION in the sentence than in the list condition. While the right IFG is occasionally active for syntactic manipulations (Tyler et al., 2010; Fiebach et al., 2005; Friederici et al., 2000), it is not frequently reported, and the aphasia literature do not support an association between deficits in sentence processing and the right IFG (Damasio, 1992). In addition, the significant effect of STRUCTURE in the ROI analyses were such that there was increased activation for the list condition – quite contrary to the expectation of a region involved in syntactic structure building. As such, the effect of PERTURBATION in this region is likely to reflect non-syntactic mechanisms deployed as a result of perturbation of syntactic structure, consistent with the observation that a previous study investigating perturbation at a lower level of language, speech production, obtained effects in a similar region in the right hemisphere (Tourville et al., 2008). The operative mechanism is likely to be action inhibition, or “stopping”, which has been attributed specifically to the right IFG (Aron et al., 2003; Swann et al., 2009; Aron et al., 2014).

Under this hypothesis, the right IFG operates as a “brake” – the inhibition of a planned action. Applying this braking hypothesis to the current study, the reverse inference is that when subjects planned to produce a sentence with a given sentence construction, they utilized the brake to inhibit this plan when the target construction changed due to perturbation; whereas when subjects planned to produce a list of words, they did not have to inhibit a plan, or relied on the brake much less. What is interesting is that in our study, the cues provided roughly equivalent information to the subjects on how to plan their utterances – e.g., *Mary is following (somebody)* in the sentence condition, *Mary word left arrow (somebody)* in the list condition, yet only during the sentence condition did they initiate a full plan, requiring the brake to stop during perturbation, whereas in the list condition they did not initiate the full plan, not requiring the brake to stop during perturbation. Speculatively, it seems that syntactic structure provides privileged access to the speech production system; in other words, the speech production system could not take advantage of the information provided during the list condition to produce a phonological/articulatory plan.

This speculation is consistent with a body of psycholinguistic evidence suggesting that syntactic structure provides benefits to speech comprehension and acoustic judgments (Miller, Heise, & Lichten, 1951; Miller, 1962; Miller, Bruner, & Postman, 1954), and that syntactic complexity has ramifications for real-time processing of sentences (Miller & McKean, 1964; Mehler, 1963; Clifton, Kurcz, & Jenkins, 1965; Clifton & Odom, 1966; Gough, 1965; Fromkin, 1971). These previous results converge to demonstrate that syntactic structure is used during sentence comprehension and production, and is useful. What our results show is that subjects not only used syntactic structure to plan their utterances according to the cues during the sentence condition, but were unable to equivalently plan their utterances during list production, even though sufficient information to plan their utterances was provided to them by the cues. Again, the speculation is that syntax has privileged access to the speech production system, consistent with its hypothesized role in providing structured linguistic objects to the sensory-motor system (Chomsky, 1982; 1995). These speculations are supported by the neuroimaging data, but are compatible with the informal observation that subjects perceived the list production condition to be unnatural, and the recordings of their behavioral data indicate longer production times and less fluent production. However, given insufficient controls between the conditions, we cannot justify any firm conclusions from this study.

4.4.4 Activations in the anterior temporal lobe (ATL)

While our whole-brain analysis did not reveal any effects in the ATL, our ROI analyses did reveal interesting differences between the sentence and list conditions. In particular, both the left and right ATL showed significant effects of STRUCTURE: increased activation to sentences over word lists. The sentence > list effect in the ATL is consistent with the literature showing this effect in sentence comprehension (Mazoyer et al., 1993; Humphries et al., 2005; 2007; Vandenberghe et al., 2002; Rogalsky & Hickok, 2009), as well as effects of basic composition at the phrasal level for comprehension and production (Bemis & Pylkkanen, 2011; Del Prato &

Pylkkanen, 2014). In addition, the ATL did not show any significant effect of perturbation, and appeared to show (although nonsignificant) *decreased* activity for the switch condition. The decreased activation is inconsistent for a basic role in syntactic operations, as perturbation would presumably *increase* demands on syntactic structure building, requiring the updating of syntactic structure, but is consistent with a role in semantic processing. It is likely that attention to semantic content was reduced during the switch condition, as subjects focused on performing the task correctly rather than interpreting the meaning of sentences. Rogalsky & Hickok (2009) showed that attention to semantic content significantly modulates activation in the sentence-preferring ATL area, consistent with this idea. In addition, the hypothesis that the ATL is involved in combinatorial semantics, but not syntax, is consistent with the lesion data discussed in the introduction (Wilson et al., 2014; Mesulam, 2013), and is compatible with neuroimaging results suggesting that the ATL prefers particular kinds of semantic composition, not syntactic phrase-structure building generally (Westerlund & Pylkkanen, 2014).

4.5 Conclusions

The present study sought to implement a novel paradigm in the study of syntax and the brain; we successfully applied the perturbation paradigm to syntactic structure, obtaining significant activations associated with our manipulation. While our activations point to a possibility of overlap in the neural organization of motor control and syntax, it is difficult to make any firm conclusions based on this study alone. The right IFG particularly responded to the perturbation manipulation in sentences rather than word lists, suggesting that producing a list of words does not involve as much phonological/articulatory planning than sentence production.

The lack of effects in Broca’s area suggest that this area performs a similar function during production of sentences and unstructured word lists, which is unlikely to be a syntactic function, particularly in combination with the other lines of evidence speaking against a role for syntax in Broca’s area. Finally, ROI analyses in the ATL indicated that this region differentiates the sentences and word lists, consistent with a role in combinatorial semantics. However, our results leave the major enigma, the neural basis for syntactic operations, largely unknown, with some hints toward a role for subcortical structures (basal ganglia and thalamus) and SMA/pre-SMA in basic structural processing for motor control and syntax.

Chapter 5

Summary & Conclusions

This dissertation consisted of two main goals: (i) to illustrate that current proposals regarding the syntax-brain relationship are inadequate, and (ii), in light of these inadequacies, to shed new light on the neural basis of syntax, the core component of human linguistic ability. I daresay that I have succeeded much more in (i) than in (ii), although it is probably a scientific law that it is easier to tear down than to build up. With that said, here are the principal findings of my investigations:

1. Distance effects in long-distance dependencies (i.e., *Movement* and *anaphora*) in Broca's area depend on how these dependencies are processed, not on their syntactic properties. Our specific empirical finding is that backward anaphora, processed actively, produce a distance effect in Broca's area, while the previous study by Santi & Grodzinsky (2007) found that forward anaphora, not processed actively, do not produce a distance effect in Broca's area.
2. The upshot of this empirical finding is that, in accord with previous authors (Kaan & Swaab, 2002; Stowe et al., 2005; Rogalsky & Hickok, 2011; Bornkessel-Schlesewsky & Schlesewsky, 2013), Broca's area is *not* the locus of syntactic operations.
3. Sentence-selectivity in Broca's area, if obtained, doesn't indicate anything particularly revelatory with respect to localizing crucial components of the language faculty: the prevalence of neuronal retuning of domain-general cognitive functions for domain-specific inputs, exemplified by research on the

visual word form area (Dehaene & Cohen, 2007), suggests that activation-selectivity is misleading with respect to the functions of interest in language.

4. In particular, in the case of Broca's area, language-specific working memory is a plausible account of sentence-specific activations in this region.
5. Syntax, in accord with previous psycholinguistic studies (e.g., Miller, 1962) appears to afford advantages to the speech production system in terms of degree of planning. These advantages, in our study, were not reducible to how much the subject could *in principle* plan, because both the sentence and list conditions afforded equal amounts of information with respect to phonological/articulatory planning.
6. Syntax may bear some interesting similarities to motor control with respect to the neural systems involved in response to perturbation and updating, in particular, the supplementary motor area, basal ganglia, and thalamus. Future research pursuing these similarities may prove fruitful in understanding the neural basis of syntax.
7. Activations in Broca's area and the ATL did not exhibit the response pattern in our syntactic perturbation study as expected of regions involved in syntactic processing.
8. The ATL exhibits the sentence > word lists effect during speech production reported in sentence comprehension (e.g., Mazoyer et al., 1993), supporting a role for combinatorial semantics in this region.

As in many other studies, the work presented here raises many questions, and provides fewer answers. Principally, it raises the question: why do we see such clear neurobiological correlates for idiosyncratic cognitive capacities, like reading in the visual word form area (Dehaene & Cohen, 2011) and face perception in the fusiform face area (Kanwisher et al., 1997), but very unclear neurobiological correlates of a central component of human cognition, syntax? Chapter 3 hinted that this difficulty lies in thinking about *what kind of* cognitive operation one is studying, and Chapter 4 suggested one alternative way of thinking about what kind of operation syntax is. The difficulty in localizing syntax may well serve as an important case study in understanding the fundamental nature of other domains of cognition and their neurobiological correlates – time alone will tell.

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APPENDIX A

Sentence stimuli from the experiment reported in Chapter 2

WH-SENTENCES

1A) Which song did the band play poorly and unenthusiastically at the concert that ended early?
1B) Which song did the band that won the contest play poorly and unenthusiastically at the concert?

2A) Which policy did the senator advise strongly and urgently during the election that interested many?
2B) Which policy did the senator that advocated gay rights advise strongly and urgently during the election?

3A) Which cookie jar did the child steal mischievously and quietly in the house that contained a lot of food?
3B) Which cookie jar did the child that loved delicious snacks steal mischievously and quietly in the house?

4A) Which event did the swimmer race skillfully and flawlessly during the Olympics that occurred last summer?
4B) Which event did the swimmer that won the gold medal race skillfully and flawlessly during the Olympics?

5A) Which car did the fugitive drive unsteadily and recklessly through the street that had heavy traffic?
5B) Which car did the fugitive that returned from hiding drive unsteadily and recklessly through the street?

6A) Which trail did the student walk regularly and unexcitedly during the summer that was extremely hot?
6B) Which trail did the student that needed a new car walk regularly and unexcitedly during the summer?

7A) Which turkey did the man cook carefully and lovingly in the kitchen that had many new appliances?
7B) Which turkey did the man that wore a silly apron and hat cook carefully and lovingly in the kitchen?

8A) Which jet did the pilot fly cautiously and secretively over the base that built nuclear weapons?
8B) Which jet did the pilot that served the air force fly cautiously and secretively over the base?

9A) Which law did the man break shamelessly and thoughtlessly during the riots that occurred in the city?
9B) Which law did the man that engaged in the protest break shamelessly and thoughtlessly during the riots?

10A) Which meal did the chef cook perfectly and effortlessly in the kitchen that received several orders?
10B) Which meal did the chef that appeared on television cook perfectly and effortlessly in the kitchen?

11A) Which routine did the clown perform humorously and gleefully at the circus that came into town?
11B) Which routine did the clown that wore a costume perform humorously and gleefully at the circus?

12A) Which food did the customer eat contently and delightfully at the restaurant that got good reviews?
12B) Which food did the customer that came for dinner eat contently and delightfully at the restaurant?

13A) Which opponent did the boxer fight aggressively and fearlessly during the championships that attracted large crowds?
13B) Which opponent did the boxer that trained all year long fight aggressively and fearlessly during the championships?

14A) Which suspect did the detective interrogate fervently and furiously during the investigation that began last weekend?
14B) Which suspect did the detective that despised criminals interrogate fervently and furiously during the investigation?

15A) Which speech did the king deliver eloquently and loudly at the ceremony that christened the new warship?
15B) Which speech did the king that feared public speaking deliver eloquently and loudly at the ceremony?

16A) Which officer did the criminal shoot violently and mercilessly in the parking lot that was near a high school?
16B) Which officer did the criminal that tried to steal a car shoot violently and mercilessly in the parking lot?

17A) Which rabbit did the dog chase frantically and excitedly through the park that allowed unleashed pets?
17B) Which rabbit did the dog that loved catching rodents chase frantically and excitedly through the park?

18A) Which album did the singer record awfully and cheaply in the studio that experienced financial troubles?
18B) Which album did the singer that recently joined a famous label record awfully and cheaply in the studio?

19A) Which stop sign did the driver run carelessly and foolishly at the intersection that had many cameras?
19B) Which stop sign did the driver that received a new license run carelessly and foolishly at the intersection?

20A) Which experiment did the scientist design ingeniously and diabolically for the military that administered unethical tests?
20B) Which experiment did the scientist that produced some controversial results design ingeniously and diabolically for the military?

21A) Which animal did the alligator attack stealthily and ravenously in the river that flowed through the forest?
21B) Which animal did the alligator that had very large teeth attack stealthily and ravenously in the river?

22A) Which barn did the farmer paint diligently and happily at the ranch that raised sheep and cows?
22B) Which barn did the farmer that raised sheep and cows paint diligently and happily at the ranch?

23A) Which flower girl did the bride kiss sweetly and sincerely at the wedding that spread tender emotion?
23B) Which flower girl did the bride that wore a white veil and dress kiss sweetly and sincerely at the

wedding?

24A) Which candy bar did the boy steal quickly and quietly from the shopkeeper that left the large counter unattended?
24B) Which candy bar did the boy that noticed the unattended counter steal quickly and quietly from the shopkeeper?

25A) Which kitten did the mother search for at the pet shop that opened last week?
25B) Which kitten did the mother that wanted a cat search for thoroughly and frantically at the pet shop?

26A) Which candy did the confectioner design naturally and rapidly during the weekend that provided much inspiration?
26B) Which candy did the confectioner that had an enormous sweet tooth design naturally and rapidly during the weekend?

27A) Which cookies did the girl scout sell warmly and intelligently at the booth that stood in front of the store?
27B) Which cookies did the girl scout that tied ribbons on the boxes sell warmly and intelligently at the booth?

28A) Which movie did the couple choose wisely and seriously at the theater that was around the corner?
28B) Which movie did the couple that wanted to see drama choose wisely and seriously at the theater?

29A) Which grandmother did the firefighter save promptly and victoriously from the house that collapsed during the fire?
29B) Which grandmother did the firefighter that performed under pressure save promptly and victoriously from the house?

30A) Which cowboy did the horse buck wildly and violently during the cattle drive that lasted five days?
30B) Which cowboy did the horse that stood big and strong buck wildly and violently during the cattle drive?

31A) Which spy did the general call cautiously and hastily during the war that erupted into chaos?
31B) Which spy did the general that wore many decorations call cautiously and hastily during the war?

32A) Which roses did the florist choose delicately and elegantly at the market that opened early every morning?
32B) Which roses did the florist that designed arrangements for banquets choose delicately and elegantly at the market?

33A) Which dog did the judge inspect properly and thoroughly at the show that occurred at the convention center?
33B) Which dog did the judge that was experienced for many years inspect properly and thoroughly at the show?

34A) Which fairy did the daughter imitate dreamily and happily at the costume party that was for a birthday?
34B) Which fairy did the daughter that wore purple everyday imitate dreamily and happily at the costume party?

35A) Which cake did the mother bake professionally and lovingly for the children that enjoyed delicious

treats?
35B) Which cake did the mother that wrote brilliant recipes bake professionally and lovingly for the children?

36A) Which salesman did the father punch suddenly and forcefully at the electronics store that had a sale?
36B) Which salesman did the father that became angry punch suddenly and forcefully at the electronics store?

37A) Which baseball did the player whack strongly and quickly during the inning that determined the winner?
37B) Which baseball did the player that won the game for the team whack strongly and quickly during the inning?

38A) Which makeup did the beautician purchase joyfully and cleverly at the supply store that opened recently?
38B) Which makeup did the beautician that wore many feathers purchase joyfully and cleverly at the supply store?

39A) Which gardener did the owner pay willingly and fully for the work that cost a lot of money?
39B) Which gardener did the owner that wanted new landscaping pay willingly and fully for the work?

40A) Which window did the kid break accidentally and guiltily during the ball game that got out of hand?
40B) Which window did the kid that hit the home run break accidentally and guiltily during the ball game?

41A) Which businessman did the criminal kidnap quickly and quietly during the incident that lasted for two days?
41B) Which businessman did the criminal that had a long record kidnap quickly and quietly during the incident?

42A) Which contractor did the engineer pay excessively and unnecessarily during the recession that lasted the whole season?
42B) Which contractor did the engineer that came up with the new plan pay excessively and unnecessarily during the recession?

43A) Which toy did the child break angrily and intensely at the daycare that separated the kids by age?
43B) Which toy did the child that disliked the other kids and staff break angrily and intensely at the daycare?

44A) Which article did the editor read slowly and cautiously during the investigation that lasted six months?
44B) Which article did the editor that wore round glasses read slowly and cautiously during the investigation?

45A) Which lesson did the instructor teach clearly and concisely to the undergraduates that were enrolled in the art class?
45B) Which lesson did the instructor that earned a degree in fine art teach clearly and concisely to the undergraduates?

46A) Which rock did the boy throw carelessly and thoughtlessly at the girl that cried for the rest of the

afternoon?
46B) Which rock did the boy that made trouble frequently at school throw carelessly and thoughtlessly at the girl?

47A) Which story did the old man tell frequently and elaborately to the reporter that worked for the newspaper?
47B) Which story did the old man that served in the war tell frequently and elaborately to the reporter?

48A) Which poem did the girl write emotionally and lovingly in the diary that held many secret thoughts?
48B) Which poem did the girl that wondered about love write emotionally and lovingly in the diary?

49A) Which camera did the man steal quickly and carefully during the burglary that lasted ten minutes?
49B) Which camera did the man that broke into the house steal quickly and carefully during the burglary?

50A) Which car did the teenager borrow quietly and secretly from the uncle that found out later?
50B) Which car did the teenager that had a hot date borrow quietly and secretly from the uncle?

51A) Which entrée did the chef cook quickly and skillfully during the dinner rush that lasted two hours?
51B) Which entrée did the chef that hated pressure cook quickly and skillfully during the dinner rush?

52A) Which symphony did the musician compose carefully and painstakingly for the art festival that lasted all spring?
52B) Which symphony did the musician that worked all the time compose carefully and painstakingly for the art festival?

53A) Which round did the boxer win skillfully and heatedly during the match that ended quickly?
53B) Which round did the boxer that broke the record win skillfully and heatedly during the match?

54A) Which apple did the cook chop urgently and expertly during the cooking contest that lasted sixty minutes?
54B) Which apple did the cook that owned a nice restaurant chop urgently and expertly during the cooking contest?

55A) Which marathon did the man run intensely and heatedly during the contest that lasted all spring?
55B) Which marathon did the man with a gold medal run intensely and heatedly during the contest?

56A) Which lap did the athlete swim urgently and breathlessly during the heat that lasted for ten seconds?
56B) Which lap did the athlete that won the competition swim urgently and breathlessly during the heat?

57A) Which command did the sergeant yell urgently and clearly to the troops that dodged the explosion?
57B) Which command did the sergeant that dodged the explosion yell urgently and clearly to the troops?

58A) Which song did the girl sing beautifully and loudly to the crowd that begged for a longer performance?
58B) Which song did the girl that exhibited amazing skill sing beautifully and loudly to the crowd?

59A) Which game did the child play excitedly and happily with the caretaker that wore a crazy hat?
59B) Which game did the child that wore a crazy hat play excitedly and happily with the caretaker?

60A) Which horse did the woman ride expertly and beautifully over the road that spanned the entire park?

60B) Which horse did the woman that sat in the small saddle ride expertly and beautifully over the road?

61A) Which car did the customer inspect diligently and neurotically at the dealership that sold used vehicles?
61B) Which car did the customer that bargained for a deal inspect diligently and neurotically at the dealership?

62A) Which drum set did the musician investigate passionately and cautiously at the shop that sold many instruments?
62B) Which drum set did the musician that sold many instruments investigate passionately and cautiously at the shop?

63B) Which candy did the owner make skillfully and proudly for the shop that made money during Christmas?
63B) Which candy did the owner that made money during Christmas make skillfully and proudly for the shop?

64A) Which tune did the aunt hum sweetly and quietly to the infant that fell asleep in the crib?
64B) Which tune did the aunt that babysat each weekend hum sweetly and quietly to the infant?

65A) Which horse did the worker pet softly and lovingly at the stable that provided excellent care?
65B) Which horse did the worker that provided excellent care pet softly and lovingly at the stable?

66A) Which coffee did the owner taste delightfully and slowly at the factory that sold exotic beans?
66B) Which coffee did the owner that sold exotic beans taste delightfully and slowly at the factory?

67A) Which software did the tech nerd steal knowingly and secretively for the company that advocated a free operating system?
67B) Which software did the tech nerd that advocated a free operating system steal knowingly and secretively for the company?

68A) Which weekend did the vacationers choose informatively and excitedly for the trip that balanced work and pleasure?
68B) Which weekend did the vacationers that planned to see New York choose informatively and excitedly for the trip?

69A) Which phone did the kid demand annoyingly and impatiently at the store that offered the largest selection?
69B) Which phone did the kid that pestered the manager each day demand annoyingly and impatiently at the store?

70A) Which tent did the camper set up quickly and imperfectly for the kids that desired a weekend of fun?
70B) Which tent did the camper that desired a weekend of fun set up quickly and imperfectly for the kids?

71A) Which gym did the athlete create energetically and enthusiastically after the announcement that declared a new training program?
71B) Which gym did the athlete that declared a new training program create energetically and enthusiastically after the announcement?

72A) Which mural did the girl paint slowly and carefully during the festival that attracted a large audience?
72B) Which mural did the girl that attracted a large audience paint slowly and carefully during the festival?

73A) Which frog did the princess kiss apprehensively and quickly in the fairy tale that ended with happiness?
73B) Which frog did the princess that dreamed of a charming prince kiss apprehensively and quickly in the fairy tale?

74A) Which fighter did the referee disqualify sternly and intently during the scene that erupted in the match?
74B) Which fighter did the referee that disapproved of low blows disqualify during the scene?

75A) Which boy did the girl steal jealously and foolishly from the girlfriend that used bad judgment?
75B) Which boy did the girl that used bad judgment steal jealously and foolishly from the girlfriend?

76A) Which house did the realtor showcase confidently and delightfully to the couple that moved away from the city?
76B) Which house did the realtor that moved away from the city showcase confidently and delightfully to the couple?

77A) Which officer did the chief promote happily and proudly at the ceremony that honored outstanding service?
77B) Which officer did the chief that noticed a big improvement promote happily and proudly at the ceremony?

78A) Which movie did the critic watch silently and uncomfortably during the screening that revealed the director's thoughts?
78B) Which movie did the critic that disliked intense horror films watch silently and uncomfortably during the screening?

79A) Which patient did the doctor treat immediately and thoroughly at the clinic that accepted any insurance policy?
79B) Which patient did the doctor that graduated from a top medical school treat immediately and thoroughly at the clinic?

80A) Which photographs did the coroner present carefully and clearly to the judge that decided the fate of the defendant?
80B) Which photographs did the coroner that handled countless corpses in the morgue present carefully and clearly to the judge?

81A) Which rabbit did the wolf devour quickly and violently in the forest that scared all the children?
81B) Which rabbit did the wolf that scared all the children devour quickly and violently in the forest?

82A) Which confession did the defendant divulge inadvertently and foolishly during the trial that defied all precedent?
82B) Which confession did the defendant that defied all precedent divulge inadvertently and foolishly during the trial?

83A) Which product did the inventor advertise aggressively and widely to the company that marketed new gadgets?
83B) Which product did the inventor that marketed new gadgets advertise aggressively and widely to the company?

84A) Which test did the apprentice fail miserably and regrettably at the end of the training that took an entire year?
84B) Which test did the apprentice that possessed great potential fail miserably and regrettably at the end of the training?

85A) Which temple did the monk protect fearlessly and passionately during the uprising that threatened the new peace?
85B) Which temple did the monk that lived in solitude protect fearlessly and passionately during the uprising?

86A) Which knight did the king favor clearly and unquestionably at the round table that seated the best royal servants?

86B) Which knight did the king that needed a worthy successor favor clearly and unquestionably at the round table?

87A) Which sword did the blacksmith forge meticulously and painstakingly for the warrior that battled mythical creatures?
87B) Which sword did the blacksmith that crafted powerful weapons forge meticulously and painstakingly for the warrior?

88A) Which marathon did the youth run vigorously and competitively during the international event that captured headlines?
88B) Which marathon did the youth that captured headlines run vigorously and competitively during the international event?

89A) Which mystery did the detective investigate cautiously and intensely in the small town that experienced strange events?
89B) Which mystery did the detective that developed strong suspicions investigate cautiously and intensely in the small town?

90A) Which land did the dictator rule tyrannically and unstoppably throughout the years that devastated millions of people?
90B) Which land did the dictator that lacked fundamental moral principles rule tyrannically and unstoppably throughout the years?

91A) Which boat did the captain sail quickly and efficiently during the campaign that drove the crew insane?
91B) Which boat did the captain that drove the crew insane sail quickly and efficiently during the campaign?

92A) Which ballad did the girl sing beautifully and softly to the crowd that became quiet quickly?
92B) Which ballad did the girl that became a sensation sing beautifully and softly during the concert?

93A) Which question did the child ask excitedly and hurriedly during the conversation that troubled the parents?

93B) Which question did the child that troubled the parents ask excitedly and hurriedly during the conversation?

94A) Which car did the man wash slowly and expertly for the customer that waited impatiently?
94B) Which car did the man that wore the blue overalls wash slowly and expertly for the customer?

95A) Which book did the teacher read quietly and intelligently to the children that took a nap in the classroom?
95B) Which book did the teacher that earned a degree in English read quietly and intelligently during the class?

96A) Which purse did the woman buy quickly and excitedly during the sale that lasted all day long?
96B) Which purse did the woman that owned a fancy car buy quickly and excitedly during the sale?

97A) Which meal did the man cook cheaply and badly during the date that disappointed the woman?
97B) Which meal did the man that had little experience cook cheaply and badly during the date?

98A) Which video game did the teenager play carefully and happily during the party that celebrated the birthday?
98B) Which video game did the teenager that destroyed many opponents play carefully and happily during the party?

99A) Which class did the professor teach interestedly and humorously in the department that taught the best students?
99B) Which class did the professor that taught the best students teach interestedly and humorously during the semester?

100A) Which race did the man run laboriously and painstakingly during the event that lasted all day?
100B) Which race did the man that broke an ankle run laboriously and painstakingly during the event?

BACKWARD ANAPHORA SENTENCES

1A) Because she decorated the wedding cake, the baker wowed the customer that made the long order.
1B) Because she decorated the wedding cake that was six layers tall, the baker wowed the customer.

2A) Because he extinguished the flames, the fireman saved the resident that arrived later.
2B) Because he extinguished the flames that burned all night long, the fireman saved the resident.

3A) Because she arranged the banquet, the planner pleased the college that loved the nice layout.
3B) Because she arranged the banquet that included few employees, the planner pleased the college.

4A) Because he mowed the grass during the summer, the son impressed the dad that held low expectations.
4B) Because he mowed the grass during the summer that was incredibly hot, the son impressed the dad.

5A) Because she fixed the sink, the housewife amazed the husband that made the repairs.
5B) Because she fixed the sink that cracked down the side, the housewife amazed the husband.

6A) Because he bought the small business, the entrepreneur met the employees that showed concern.
6B) Because he bought the small business that sold used books, the entrepreneur met the employees.

7A) Because she delivered the baby during the night, the nurse greeted the family that came from out of town.
7B) Because she delivered the baby during the night that became very busy, the nurse greeted the family.

8A) Because he kicked the winning goal during the game, the player waved to the fan that hung over the bleachers
8B) Because he kicked the winning goal during the game that won the championship, the player waved to the fan.

9A) Because she gathered the kids during camp, the councilor sang with the musician that played the guitar.
9B) Because she gathered the kids during camp that lasted two months, the councilor sang with the musician.

10A) Because he rescued the kitten from the tree, the neighborhood boy found the owner that put up all the posters.
10B) Because he rescued the kitten from the tree that hung over the back yard, the neighborhood boy found the owner.

11A) Because she painted a beautiful picture, the artist thanked the curator that awarded the honor.
11B) Because she painted a beautiful picture that showed the vast ocean, the artist thanked the curator.

12A) Because he played guitar in a rock band, the musician thanked the writer that wrote the song.
12B) Because he played guitar in a rock band that went on tour, the musician thanked the writer.

13A) Because she won the event, the gymnast thanked the coach that provided the training.
13B) Because she won the event that tested all the athletes, the gymnast thanked the coach.

14A) Because he discovered the new vaccine, the researcher cured the disease that ravaged the country.
14B) Because he discovered the new vaccine that fought off the virus, the researcher cured the disease.

15A) Because he loved video games, the boy thanked the developer that made the new game.
15B) Because he loved playing video games that were exciting, the boy thanked the developer.

16A) Because she wrote a new novel, the writer thanked the publisher that quickly printed the book.
16B) Because she wrote a new novel that became quickly well known, the writer thanked the publisher.

17A) Because she performed beautifully during the show, the singer thanked the writer that created the musical.
17B) Because she performed beautifully during the show that dazzled the large audience, the singer thanked the writer.

18A) Because he attended the opening ceremony, the speaker thanked the president that sent the invitation.
18B) Because he attended the opening ceremony that marked the new expansion, the speaker thanked the president.

19A) Because he was running for the office, the lawyer raised funds for the campaign that needed money badly.
19B) Because he was running for the office that opened in November, the politician raised funds for the

campaign.

20A) Because she was learning a new language, the mother thanked the teacher that provided the lessons.
20B) Because she was learning a new language that provided challenges, the mother thanked the teacher.

21A) Because he scored many touchdowns during the Super Bowl, the player pleased the coach that orchestrated the winning play.
21B) Because he scored many touchdowns during the Super Bowl that ended very recently, the player pleased the coach.

22A) Because he completed major transactions for the company, the businessman impressed the manager that wanted quick results.
22B) Because he completed major transactions for the company that sold electronics, the businessman impressed the manager.

23A) Because he enacted thrilling scenes in the movie, the stuntman amazed the director that offered the lead role.
23B) Because he enacted thrilling scenes in the movie that used huge explosives, the stuntman amazed the director.

24A) Because he partied relentlessly throughout the summer, the bachelor entertained the guest that looked for a good time.
24B) Because he partied relentlessly throughout the summer that was extremely hot, the bachelor entertained the guest.

25A) Because she danced beautifully at the recital, the ballerina admired the instructor that taught challenging routines.
25B) Because she danced beautifully at the recital that challenged the performers, the ballerina admired the instructor.

26A) Because he hosted the awards ceremony, the comedian announced the nominee that won the best performance award.
26B) Because he hosted the awards ceremony that captured all of the attention, the comedian announced the nominee.

27A) Because he worked at weddings for a career, the cameraperson photographed the couple that offered the job.
27B) Because he worked at weddings for a career that lasted eight years, the cameraperson photographed the couple.

28A) Because he completed several quality facelifts, the doctor assured the client that feared the scary procedure.
28B) Because he completed several quality facelifts that got excellent approval, the doctor assured the client.

29A) Because he successfully repaired the toilet, the plumber billed the homeowner that added a generous tip.
29B) Because he successfully repaired the toilet that malfunctioned quite suddenly, the plumber billed the homeowner.

30A) Because he cooked an extraordinary meal at the restaurant, the chef surprised the critic that loved

the house special.
30B) Because he cooked an extraordinary meal at the restaurant that reopened in May, the chef surprised the critic.

31A) Because she was making dinner, the wife thanked the maid that helped with the preparations.
31B) Because she was making a dinner that consisted of five courses, the wife thanked the maid.

32A) Because he was going to the local jail, the man hated the judge that delivered the sentence.
32B) Because he was going to the local jail that held many criminals, the man hated the judge.

33A) Because he was having a barbeque, the man invited the neighbor that prepared the meat excellently.
33B) Because he was having a barbeque that celebrated the holiday, the man invited the neighbor.

34A) Because she was getting a cold, the girl thanked the doctor that prescribed the medicine.
34B) Because she was getting a cold that blocked all air from the nose, the girl thanked the doctor.

35A) Because he wanted to become a teacher, the man thanked the professor that sent the letter.
35B) Because he wanted to become a teacher that cared for students, the man thanked the professor.

36A) Because he divulged confidential information to the enemy, the spy betrayed the agency that operated in secrecy.
36B) Because he divulged confidential information to the enemy that prepared the malicious plans, the spy betrayed the agency.

37A) Because he captured the boar in the jungle, the hunter fed the tribe that wanted a good meal badly.
37B) Because he captured the boar in the jungle that became scarce in food supply, the hunter fed the tribe.

38A) Because he destroyed the sand castle at the beach, the surfer infuriated the child that worked for several hours.
38B) Because he destroyed the sand castle at the beach that brimmed with visitors, the surfer infuriated the child.

39A) Because he committed countless crimes, the perpetrator appalled the judge that gave a punishment of life in prison.
39B) Because he committed countless crimes that included homicide and kidnapping, the perpetrator appalled the judge.

40A) Because he solved a challenging puzzle, the student excited the instructor that welcomed worthy competitors.
40B) Because he solved a challenging puzzle that required extensive practice, the student excited the instructor.

41A) Because she applied a cheap dye, the hairdresser disappointed the entertainer that attended the rock concert.
41B) Because she applied a cheap dye that cost very little money, the hairdresser disappointed the entertainer.

42A) Because he spoke unclearly during the presentation, the lecturer confused the audience that ignored the entire conclusion.
42B) Because he spoke unclearly during the presentation that included complicated topics, the lecturer

confused the audience.

43A) Because he screamed loudly at the game, the fan annoyed the spectator that sat directly in front.
43B) Because he screamed loudly at the game that caused quite a commotion, the fan annoyed the spectator.

44A) Because he arrived late to the meeting, the executive blamed the driver that forgot the car in the garage.
44B) Because he arrived late to the meeting that occurred once a month, the executive blamed the driver.

45A) Because he finished the latest design, the architect notified the contractor that led the construction project.
45B) Because he finished the latest design that looked very innovative, the architect notified the contractor.

46A) Because he filmed a controversial movie, the director offended the viewer that expected something else.
46B) Because he filmed a controversial movie that depicted graphic scenes, the director offended the viewer.

47A) Because he possessed a powerful weapon, the sorcerer frightened the adversary that evaded the battle.
47B) Because he possessed a powerful weapon that could vaporize objects, the sorcerer frightened the adversary.

48A) Because he wrecked the car, the teenager enraged the father that paid for higher insurance fees.
48B) Because he wrecked the car that had a new paint job and tires, the teenager enraged the father.

49A) Because he conducted an unethical experiment, the scientist disappointed the colleague that had good recommendations.
49B) Because he conducted an unethical experiment that risked psychological harm, the scientist disappointed the colleague.

50A) Because he reviewed the paper, the editor advised the author that entered a contest for a scholarship.
50B) Because he reviewed the paper that advanced a completely new theory, the editor advised the author.

51A) Because she hated insects, the home owner called the exterminator that came right away.
51B) Because she hated insects that had little legs, the home owner called the exterminator.

52A) Because he left early from the office, the businessman avoided the boss that kept track of timecards.
52B) Because he left early from the office that stayed open longer, the businessman avoided the boss.

53A) Because she arrived late to the class, the girl talked to the headmaster that caught late students.
53B) Because she arrived late to the class that started early, the girl talked to the headmaster.

54A) Because he fixed the garage door, the handyman billed the homeowner that needed the repair.
54B) Because he fixed the garage door that crashed down on the car, the handyman billed the homeowner.

55A) Because she painted the artwork, the artist impressed the collector that wanted to see more pieces.

55B) Because she painted the artwork that stretched from the floor to the roof, the artist impressed the collector.

56A) Because he grew watermelons, the farmer met the vendor that sold fruit at the market**.**
56B) Because he grew watermelons that looked heavy and juicy, the farmer met the vendor.

57A) Because she skillfully decorated the backpack, the high school student amazed the friend that loved the gift.
57B) Because she skillfully decorated the backpack that was quite large, the high school student amazed the friend.

58A) Because he spent the night in the forest, the boy scout saluted the leader that presented the new badge.
58B) Because he spent the night in the forest that sheltered wild animals, the boy scout saluted the leader.

59A) Because she taught the second graders, the teacher accepted the help that alleviated the work.
59B) Because she taught the second graders that created mischief in class, the teacher accepted the help.

60A) Because he followed the bug, the toddler ignored the mother that was watching.
60B) Because he followed the bug that had blue wings, the toddler ignored the mother.

61A) Because she planted the tulips, the gardener instructed the nanny that learned the helpful tips.
61B) Because she planted the tulips that were yellow and orange, the gardener instructed the nanny.

62A) Because he fought the bear, the camper visited the nurse that bandaged the cuts.
62B) Because he fought the bear that stood on two legs, the camper visited the nurse.

63A) Because she fell off the treadmill at the gym, the athlete saw the doctor that prescribed some pain killers.
63B) Because she fell off the treadmill at the gym that serviced wealthy clients, the athlete saw the doctor.

64A) Because he saved the small boy, the doctor assured the family that worried excessively.
64B) Because he saved the small boy that worried excessively, the doctor assured the family.

65A) Because she painted the mural, the art student astonished the teacher that assigned the project.
65B) Because she painted the mural that covered the wall, the art student astonished the teacher.

66A) Because he cheated on the test, the student feared the principal that controlled detention.
66B) Because he cheated on the test that decided the grades, the student feared the principal.

67A) Because she designed clothes for celebrities, the stylist dressed the first lady that enjoyed bright colors.
67B) Because she designed clothes for celebrities that walked the red carpet, the stylist dressed the first lady.

68A) Because he harvested oranges for juice companies, the farmer negotiated with the business man that operated in the city.
68B) Because he harvested oranges for juice companies that operated in the city, the farmer negotiated with the business man.

69A) Because she created beautiful costumes for the actor, the designer impressed the director that won the award.
69B) Because she created beautiful costumes for the actor that won the award, the designer impressed the director.

70A) Because he directed a powerful movie, the student interested the executive that owned the production studio.
70B) Because he directed a powerful movie that depicted dangerous villains, the student interested the executive.

71A) Because she organized the play for the theater, the woman called the trustee that paid for the productions.
71B) Because she organized the play for the theater that put on live musicals, the woman called the trustee.

72A) Because he loved playing scrabble for the team, the nerd beat the player that made more spelling mistakes.
72B) Because he loved playing scrabble for the team that had eleven members, the nerd beat the player.

73A) Because she sang in a band, the nanny entertained the children that enjoyed the soft music.
73B) Because she sang in a band that performed mostly oldies, the nanny entertained the children.

74A) Because she loved to play music, the girl respected the composer that won the prestigious award.
74B) Because she loved to play music that excited the listener, the girl respected the composer.

75A) Because she worked for the airline, the flight attendant served the businessmen that operated around the world.
75B) Because she worked for the airline that operated around the world, the flight attendant served the businessmen.

76A) Because he wrote picture books for children, the illustrator impressed the father that struggled with writing.
76B) Because he wrote picture books for children that struggled with reading, the illustrator impressed the father.

77A) Because she sold greeting cards, the shopkeeper flattered the customer that walked into the store.
77B) Because she sold greeting cards that played music and songs, the woman flattered the customer.

78A) Because he fixed cars for customers, the mechanic argued with the supplier that forgot the motor oil.
78B) Because he fixed cars for customers that needed oil desperately, the mechanic argued with the supplier.

79A) Because she fell asleep at the meeting, the secretary apologized to the manager that led the conversation.
79B) Because she fell asleep at the meeting that discussed new directions, the secretary apologized to the manager.

80A) Because he owned a restaurant, the chef yelled at the critic that wrote a terrible review.
80B) Because he owned a restaurant that served elaborate French cuisine, the chef yelled at the critic.

81A) Because he organized the bookshelf in the corner, the volunteer assisted the librarian that requested help.
81B) Because he organized the bookshelf in the corner that collected dust, the volunteer assisted the librarian.

82A) Because he smacked the baseball over the fence, the batter energized the crowd that cheered exuberantly.
82B) Because he smacked the baseball over the fence that extended ten feet high, the batter energized the crowd.

83A) Because she watched the children, the mom called the husband that helped with the chores.
83B) Because she watched the children that complained often, the mom called the husband.

84A) Because he shattered glass on the apartment building, the vandal upset the tenant that rented the new property.
84B) Because he shattered glass on the apartment building that neighbored a poor area, the vandal upset the tenant.

85A) Because he killed the panda in the mountains, the poacher outraged the activists that protected endangered species.
85B) Because he killed the panda in the mountains that sheltered various animals, the poacher outraged the activists.

86A) Because he flushed the cocaine before the raid, the drug dealer outwitted the police that lacked sufficient evidence.
86B) Because he flushed the cocaine before the raid that occurred in the afternoon, the drug dealer outwitted the police.

87A) Because he slept through the alarm, the roommate missed the bus that went to campus every hour.
87B) Because he slept through the alarm that rang loudly all morning long, the roommate missed the bus.

88A) Because he fled the country during the war, the refugee abandoned the family that remained behind enemy lines.
88B) Because he fled the country during the war that ravaged all the major cities, the refugee abandoned the family.

89A) Because he worked at the shopping center, the security guard captured the burglar that stole the expensive merchandise.
89B) Because he worked at the shopping center that sold the expensive merchandise, the security guard captured the burglar.

90A) Because he lost everything at the casino, the gambler begged the loan shark that demanded repayment.
90B) Because he lost everything at the casino that catered to high rollers, the gambler begged the loan shark.

91A) Because he attended the university, the tutor helped the boy that struggled with algebra class.
91B) Because he attended the university that encouraged student outreach, the tutor helped the boy.

92A) Because she taught the students, the teacher disciplined the child that distracted the class with

comments.
92B) Because she taught the students that listened to instructions poorly, the teacher disciplined the child.

93A) Because he outperformed the brothers during the regime, the prince succeeded the king that battled a terminal illness.
93B) Because he outperformed the brothers during the regime that called for a capable leader, the prince succeeded the king.

94A) Because he struck the match in the brush, the arsonist started a fire that burned down the entire countryside.
94B) Because he struck the match in the brush that was just two miles away from the town, the arsonist started a fire.

95A) Because he left the building, the fireman dodged the debris that plunged down from the ceiling.
95B) Because he left the building that suffered from the earthquake, the fireman dodged the debris.

96A) Because he disliked children, the man argued with the wife that wanted a large family.
96B) Because he disliked children that complained all of the time, the man argued with the wife.

97A) Because he painted fine art, the artist thanked the collector that purchased an expensive picture.
97B) Because he painted fine art that sold frequently at the auction, the artist thanked the collector.

98A) Because he liked fine meals, the chef pleased the guests that enjoyed the roast duck.
98B) Because he liked fine meals that called for much hard work, the chef pleased the guests.

99A) Because he worked a long shift, the sheriff appreciated the wife that watched all the kids.
99B) Because he worked a long shift that tired all the cops, the sheriff appreciated the wife.

100A) Because she despised animal cruelty, the veterinarian praised the activist that ran the new dog shelter.
100B) Because she despised animal cruelty that resulted in injured dogs, the veterinarian praised the activist.

ANOMALOUS SENTENCES: WH

1) Which horse did the lawyer advise quickly and discretely during the press event that shocked the country?
2) Which parking lot did the athlete that worked extremely hard perform unsteadily and uncertainly during the event?
3) Which coffee shop did the teenager drive quickly and dangerously into the intersection that had new cameras?
4) Which tiger did the janitor clean up slowly and unhappily at the business that fired many employees?
5) Which building did the champion defeat fearlessly and totally during the exhibition that raised a lot of money?
6) Which novel did the sheriff that spent many years on the force detain calmly and appropriately at the checkpoint?
7) Which boy did the thief that needed to pay off debts steal thoughtlessly and hurriedly from the convenience store?
8) Which portrait did the apprentice serve zealously and faithfully at the institute that trained all the best scientists?

9) Which word did the lion that had sharp claws stalk slowly and methodically in the grass?
10) Which continent did the gunslinger outsmart ingeniously and unexpectedly during the confrontation that scared the entire town?
11) Which counties did the student that learned the importance of hard work sell warmly and effectively at the table?
12) Which mountain did the girl dress nicely and colorfully at the bridal shower that entertained all the guests?
13) Which country did the beggar that had little money receive happily and enthusiastically from the generous stranger?
14) Which stadium did the child drop foolishly and predictably before the coach that expected better performance?
15) Which infant did the mechanic that performed many repairs fix quickly and flawlessly for the company?
16) Which house did the man seduce sweetly and deviously during the date that turned bad quickly?
17) Which poem did the athlete that won the competition jump breathlessly and amazingly during the race?

ANOMALOUS SENTENCES: BACKWARD ANAPHORA

1) Because he fended off the wolves, the snowman rescued the deer that fled through the forest.
2) Because she repaired the flat tire that stranded the vehicle, the wrench astonished the passenger.
3) Because he played the drums for the fundraiser, the guitar received applause from the attendees that loved the performance.
4) Because she won the primary that determined the candidates, the podium thanked the campaign manager.
5) Because he discovered the solution to the problem, the microscope won the grant that funded research for three years.
6) Because he loved computers that had new software, the hard drive thanked the assistant.
7) Because she created a fantastic story, the cow thanked the producer that developed the film.
8) Because she executed the command that silenced the opposition, the stage pleased the general.
9) Because he vetoed the bill, the plant angered the congress that crafted the legislation.
10) Because he went to prison, the zebra contacted the gang that organized the escape.
11) Because he proctored the test that lasted for two hours, the hotdog went to the bar.
12) Because she went to the carnival, the balloon saw the sideshow that featured the trained animals.
13) Because he wanted to become an accountant that made lots of money, the squirrel took the difficult exam.
14) Because he loved cartoons, the camera enjoyed the character that hunted rabbits in the forest.
15) Because he crashed the bus that required many repairs, the steering wheel paid the expensive ticket.
16) Because he judged the contest, the money awarded the challenger that beat the other competitors.
17) Because he performed health inspections, the pig met the manager that oversaw food production at the store.
18) Because he examined the lizard that had an unusual color, the bench classified the new species.
19) Because he was an expert at hiking, the ostrich gave instructions to the children that followed closely behind.
20) Because he kicked the student in the knee that swelled up quickly, the pencil reported to the teacher.
21) Because he repaired airplanes, the poodle argued with the company that demanded service quickly.
22) Because he built the cupboard that required much labor, the dish impressed the woman.
23) Because he felt sick in the morning, the computer ditched the class that started early.

APPENDIX B

Verbs used in the experiment reported in Chapter 4

Admire
Deceive
Examine
Follow
Frighten
Greet
Harass
Help
Hug
Kick
Kiss
Pinch
Poke
Protect
Punch
Push
Rob
Scare
Tease
Tickle