

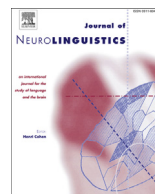


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### Review

# The functional neuroanatomy of serial order in language



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#### ABSTRACT

The paper aims to shed light on how serial order is computed in the human mind/brain, focusing on the nature of linearization in language. Linearization is here understood as the mapping of hierarchical syntactic structures onto linear strings. We take as our point of departure the now well-established need to subdivide Broca's region into different areas, and claim that these brain areas play important and distinct roles in the context of linearization. Crucially, for this mapping to be valid, linearization must be decomposed into a series of distinct (generic) sub-operations. Thus, the present work highlights the benefit of decomposing Broca's area and the linearization algorithm in parallel to formulate linking hypotheses between mind and brain.

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## 1. Introduction

The aim of the present paper is straightforward: we wish to highlight the benefits of decomposing both anatomical regions like 'Broca's area' and computational operations such as 'linearization' in language in order to formulate productive linking hypotheses across the fields of neuroscience and linguistic theory. In so doing, we hope to provide a concrete illustration of the research strategy

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advocated by David Poeppel in several publications (Poeppel, 2005, 2011, 2012; Poeppel & Embick, 2005) in an attempt to overcome the challenge of interdisciplinary exchange between theoretical linguistics and neuroscience.

Far from denying the historical usefulness of the so-called “classical model” for neurolinguistics (with Broca’s area and Wernicke’s area as landmarks), we agree with a growing number of researchers that figuring out how linguistic computation is implemented in the human brain requires us to go beyond this standard model, and recognize that regions like Broca’s region are (i) far from monolithic, (ii) just one node in a complex functional network, (iii) unlikely to be exclusively dedicated to certain cognitive domains.

In parallel, we also believe that in order for linguistic theory to inform research in neuroscience, as it should, it must provide theoretical constructs (i.e., computational operations) of the right granularity. In David Poeppel’s own words (2005, 11), “Linguists ... owe a decomposition (or fractionation) of the particular linguistic domain in question (e.g., syntax) into formal operations that are, ideally, elemental and generic .... Generic formal operations at this level of abstraction can form the basis for more complex linguistic representation and computation”.

This paper is meant as an illustration of the usefulness of taking both perspectives seriously (the one from neuroscience about “Broca’s area” and the one from linguistics concerning computational processes), by highlighting a potential convergence in the domain of linearization: how hierarchical syntactic structure is processed and mapped onto linear strings. Specifically, we claim that the decomposition of Broca’s region independently put forth in works to be reviewed below matches the decomposition of ‘linearization’ (the operation converting hierarchical structures onto linear sequences) advocated in certain theoretical linguistic models.

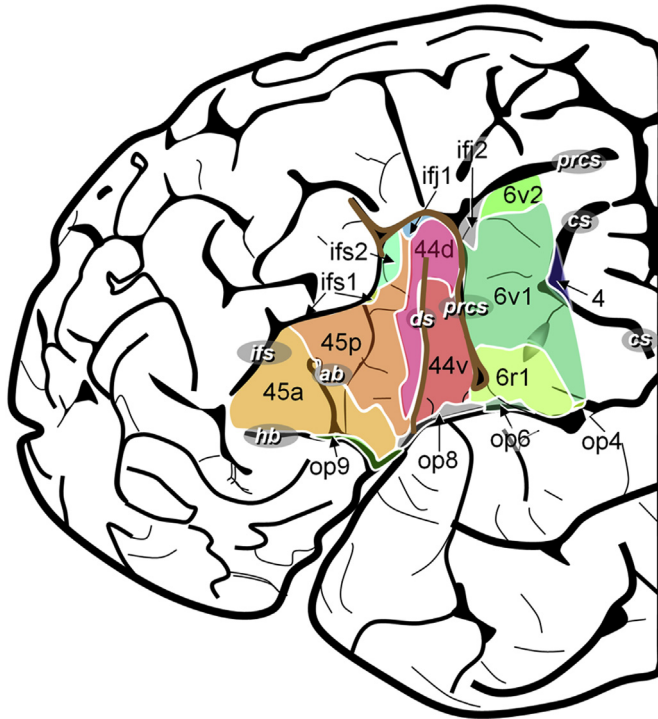
We will present both decomposition claims in parallel, and then relate the two. We will then conclude by mentioning certain testable predictions made by our hypothesis, and by addressing certain broader issues concerning the neural implementation of linguistic functions. Lest our point be misunderstood, the novelty of our hypothesis does not lie in the claim that aspects of morpho-syntax and morpho-phonology are processed in Broca’s region. Nor does it lie in the identification of linearization as a central operation computed in that region, as several works have already suggested, for example, Bornkessel, Zysset, von Cramon, Friederici, and Schlesewsky (2005), Grewe et al. (2006), Fitch and Martins (2014), and references therein. Rather, the novelty of our hypothesis lies in the claim that in order for linearization to be assigned to Broca’s region, *both* the linearization operation and Broca’s region must be further decomposed. Also, in departure from attempts to link Broca’s region to syntax, but in accordance with the model put forth in Bornkessel-Schlesewsky and Schlesewsky (2013), and the reflections in Petersson, Folia, and Hagoort (2012), we claim that Broca’s subregions process syntactic representations assembled ‘elsewhere’ in the brain.

## 2. Broca’s region: anatomy and connectivity

Broca’s region is defined anatomically as the lateral posterior two-thirds of the left inferior frontal gyrus (IFG) in the human brain. Broca’s region includes Brodmann’s cytoarchitectonic areas (BA) 44 and 45, occupying the pars opercularis and pars triangularis of the inferior frontal gyrus (IFG) in the left hemisphere, respectively. Apart from differences in the cytoarchitecture of both areas, whereas BA44 is a dysgranular area, BA45, a well-developed granular layer 4 (it is “granular”). Broca’s region also includes the base of the opercular part, also referred to as the deep frontal operculum (FO).

Receptoarchitectonic analyses have shown a subdivision of Broca’s region itself as well as a subdivision of both 44 and 45 areas (see e.g. Amunts et al., 2010; Neubert, Mars, Thomas, Sallet, & Rushworth, 2014; Zilles & Amunts, 2009). According to these receptoarchitectonic analyses, BA45 is subdivided into two different regions, a more anterior portion (45a) bordering BA47 and a more posterior portion (45p) bordering BA44. Moreover, BA44 is subdivided into a dorsal portion (44d) and a ventral portion (44v). These subdivisions are depicted in Fig. 1.

Besides this cortical architecture of Broca’s region, several authors have distinguished between a dorsal pathway and a ventral pathway connecting Broca’s region to other parts of the brain. For example, according to Friederici (2011), BA 44 connects to the posterior temporal lobe via a dorsal pathway (her so-called “Dorsal Pathway II”, which includes the arcuate fasciculus (AF) and the superior



**Fig. 1.** Extent of delineated areas projected to the lateral surface of an individual postmortem brain (reproduced from [Amunts et al., 2010](#)). 6v1 and 6v2 are ventrally located areas within BA6. 6r1 is located between BA6 and BA44. Area ifs1 is located in the inferior frontal sulcus, areas ifj1 and ifj2 are positioned at the junction of the inferior frontal and the precentral sulcus. Areas op8 and op9 are located in the deep FO. Medio-ventrally, opercular area op 6 is adjacent to 6r1.

longitudinal fasciculus (SLF). The Dorsal Pathway I runs from the premotor cortex (BA6) to the posterior temporal cortex via the AF and SLF). BA 45 connects to the anterior temporal lobe ventrally, via the extreme fiber capsule system (EFCS). This ventral pathway is also referred to as the “Ventral Pathway I” in [Friederici \(2011\)](#), to distinguish it from the “Ventral Pathway II”, which runs from FO to the anterior temporal cortex via the uncinate fasciculus (UF) ([Anwander, Tittgemeyer, Cramon, Friederici, & Knosche, 2007; Friederici, 2011](#)). [Fig. 2](#) reproduces the major aspects of Friederici's model, indicating the three regions of interest here (BA44, BA45, and frontal operculum), as well as their connections to the temporal lobe.

Even if there is disagreement in the literature about the functional significance of these pathways, there is definitely a growing consensus for the need to distinguish between a dorsal route and a ventral route, with each one dedicated to the transfer of different types of information, and endowed with distinct mechanisms of information processing (see [Bornkessel-Schlesewsky & Schlesewsky, 2013](#)).

We will return below to important issues concerning the dorsal and ventral pathways, which will lead us to depart from key aspects of [Friederici's \(2011\)](#) model, and adopt a framework like that of [Bornkessel-Schlesewsky and Schlesewsky \(2013\)](#). In the discussion that follows, we will focus mainly on Broca's region, which is comparatively better understood, but we will also have things to say about the temporal lobe. For now, let us note that given the complexity just reviewed, one should not predict “Broca's region” to do a single thing. Indeed, one should expect the many—at times, seemingly conflicting—roles ascribed to this region in the literature (see [Rogalsky & Hickok, 2011](#) for a review; [Fedorenko, Duncan, & Kanwisher, 2012](#)). When we discuss the roles of sub-areas of Broca's region below, we want the reader to remember that we do not intend to claim that this is the only thing that these sub-areas do. All we will claim is that in the context of language, the role of these sub-areas may

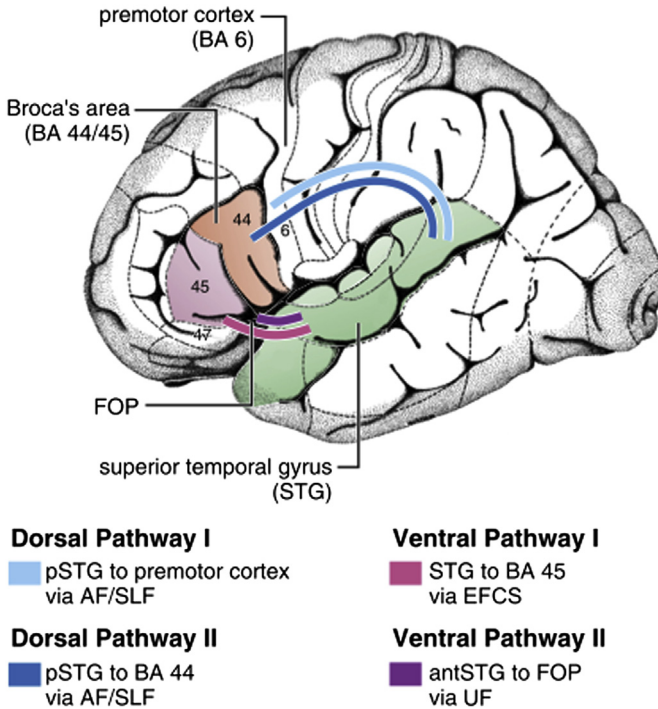


Fig. 2. Broca's region and pathways to the temporal lobe. Adapted from [Friederici, 2011](#).

be the ones we put forth. We think that it is likely, given the generic character of the computations we will ascribe to these sub-areas, that they are not exclusively linguistic in nature, and that domain-specificity is the result of the context of (dynamic) connectivity in which these computations take place.

### 3. Linearization

In the context of language processing, although speech perception would lead us to think of sentences as mere linear strings made of concatenation of words, it is well established that abstract hierarchical structures are necessary to capture the properties of language ([Chomsky, 1957](#)). Words in a sentence are definitely not beads on a string. How the hierarchies that linguists represent in tree diagrams are associated with the linear sequences speakers perceive and produce is not yet well understood. This is but a reflection of a larger problem made famous by [Lashley \(1951\)](#): the problem of serial order in behavior (for a recent overview, see [Fitch & Martins, 2014](#)).

In the domain of language, progress has been made at what [Marr \(1982\)](#) called the computational level. The mechanism by which hierarchical structures that capture the basic properties of language are mapped onto linear string is defined as the linearization procedure. This process reduces a multi-dimensional linguistic structure onto a one-dimensional lineal sequence. [Kayne's \(1994\)](#) restrictive theory of linearization denied the standard assumption in generative grammar that Universal Grammar allows a given hierarchical representation to be associated with more than one linear order. According to this theory, hierarchical structure directly determines linear ordering, in a single step (his Linear Correspondence Axiom). According to the present proposal, which relies on theoretical reflections such as [de Vries \(2009\)](#), [Bye and Svenonius \(2012\)](#), [Arregi and Nevins \(2012\)](#) and especially

Idsardi and Raimy (2013), such a direct association between hierarchical phrase structure and linear order is considered incorrect. Instead, a multi-step linearization algorithm is assumed.

Before providing the algorithm, let us make an important caveat: as is common in the generative literature, we will present the algorithm in a ‘derivational’ fashion (step 1, then step 2, etc.), but it is important for us to note that our claim does not rely on the specific order of operation, but rather on the existence of several sub-operations involved in linearization. With Hornstein (2009, p. 171f.), we think that the abstract order contained in algorithms like the one we present ought to be reversible, so as to be compatible with both production and comprehension. In fact, we think that the algorithm we are about to discuss could be implemented in a parallel architecture of the sort advocated in Jackendoff (2002). Accordingly, we ask the reader not to put too much stake into phrases like first, second, etc. in the following paragraphs. We return to the issue of ‘time’, ‘space’ and ‘function’ in Section 5. (As Bornkessel-Schlesewsky & Schlesewsky, 2013 note, the areas we will be dealing with display bi-directional neural connections, which may well provide the relevant neural substrate for the kind of reversibility that Hornstein discusses.)

Having said this, the simplest way we know of to present the need for a multi-step algorithm relies on a conception of the lexicon of the sort advocated in a theoretical framework like Distributed Morphology (DM). According to DM, there is a single generative engine for the formation of both phrases and words and there is no Lexicon in the sense that this notion has in traditional generative grammar and in numerous neurolinguistic studies (i.e. the Lexicon as a repository of lexical items that syntax operates upon to build phrases). Rather, according to DM, there are three relevant lists: the Lexicon in the narrow sense, the Vocabulary, and the Encyclopedia (Lists 1, 2, and 3 respectively in Fig. 3). Items from these lists enter the derivation at different stages, as shown schematically below. DM assumes that syntax itself generates and manipulates an unordered hierarchy of abstract syntactic features devoid of phonological content, the so-called “morphemes” (Halle & Marantz, 1993). Morphemes make up the lexicon in the narrow sense (List 1). Such abstract feature bundles must, of course, receive phonological content, an operation that is called ‘Vocabulary Insertion’ in DM. The phonological content is drawn from the Vocabulary (List 2). They must also receive semantic interpretation, coming from the resources of the Encyclopedia (List 3).

From this brief description it should already be clear to readers that one of the distinct advantages of a framework like DM in the context of cognitive science is the very real possibility DM offers to conceive of syntactic structure building as divorced from the specific properties of words. Thus, as argued in Boeckx (2014), DM opens the door to syntax being shared across cognitive domains (language, music, action, etc.), even if the minimal units manipulated in these domains differ.

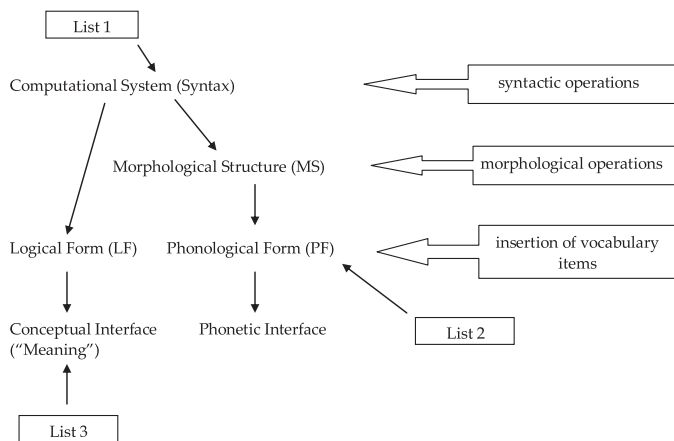


Fig. 3. The model of grammar in DM.

Adapted from Pfau, 2009, p. 65, following Halle & Marantz, 1993; Harley & Noyer, 2003.

Our main focus here is on the portion of the derivation at which abstract feature bundles manipulated in syntax receive phonological content, and are arranged into sequences fit for pronunciation. We will refer to this as the linearization stage.

According to the most explicit treatment of linearization in the DM tradition (Idsardi & Raimy, 2013), at least three steps must be distinguished to convert hierarchical structures made up of abstract feature bundles into strings with phonological content. First, syntactic manipulation must stop: the syntactic structures must be ‘immobilized’. No further syntactic manipulations (i.e. reorderings, ‘movements’, etc.) must be allowed, adjacency relations must be defined and recorded and, in the case of structural ambiguities, unique representations must be chosen. Metaphorically speaking, the syntactic representation must be ‘frozen’, as if one were to take a snapshot of a target in motion. In the second step, called Vocabulary Insertion, specific vocabulary items must compete for selection and insertion into the abstract slots that syntax has provided. In other words, morpho-phonological content must be grafted onto the hierarchical and adjacency relations that were present in the previous step. Finally, a total linear order among all the vocabulary items must be computed. This last step is called Serialization.

This is summarized in Table 1.

The most important thing for us here is that under a framework like DM, the linearization operation is not a monolithic, unified operation.

#### 4. Converging decompositions

It is plausible to suspect that unlike single-step linearization models like Kayne (1994), multi-step algorithm such as the one in Table 1 will recruit distinct brain structures and pathways. This is the idea that we want to develop in this section.

Building on the insights of Friederici (2011), we examine here whether three of the neural pathways depicted in Fig. 2 are the neurobiological substrate of such computational operations described in the previous section. Concretely, the present proposal we put forth is that (i) the dorsal pathway connecting pars opercularis (BA44) to the posterior STG via the AF/SLF subserves the Immobilization operation, (ii) the ventral pathway running from pars triangularis (BA45) to STG/MTG via the EFCS (Ventral Pathway I) is involved in Vocabulary Insertion processes, and (iii) the ventral pathway relating FO with STG/MTG (Ventral Pathway II) is related to Serialization. Fig. 4 provides a schematic representation of our proposal.

Our mapping is motivated by the following two broad considerations: since there is a linearization stage where the processing of hierarchical structure is blind to phonological content (Immobilization), we predict that the brain area responsible for it ought to be not only involved in language specific tasks, which crucially depend on phonological content, but also in more general functions dealing with the processing of hierarchical structures. Second, we predict that the brain area involved in the insertion of morpho-phonological content, ought to relate to lexical semantic processes. We believe that this is indeed what we find in the context of BA44 and BA45, as well as what we currently know about the temporal lobe.

**Table 1**  
Linearization sub-operations.

Module	Characteristics
<i>Narrow syntax</i> LINEARIZATION-1 = <b>immobilization</b>	Hierarchy, no linear order, no phonological content
<i>Morphosyntax</i> LINEARIZATION-2 = <b>spell-out</b>	Hierarchy, adjacency, no phonological content
<i>Morphophonology</i> LINEARIZATION-3 = <b>serialization</b>	No hierarchy, directed graph, phonological content
<i>Phonology</i>	No hierarchy, linear order, phonological string

From Idsardi & Raimy, 2013.

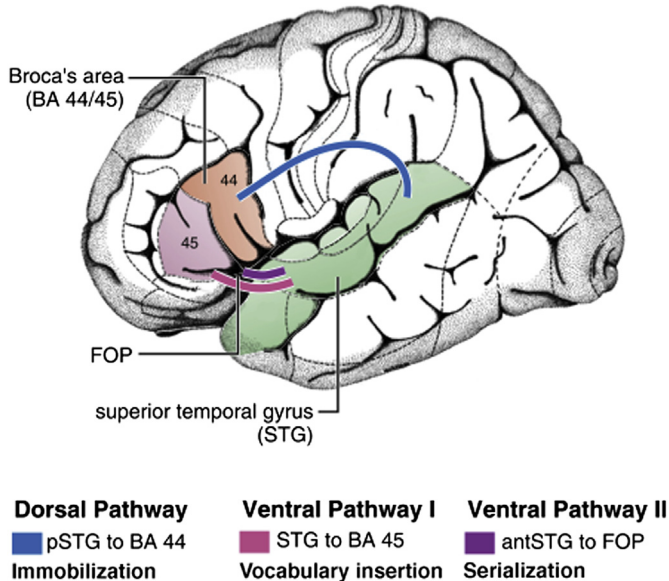


Fig. 4. Mapping a multi-step linearization algorithm onto the brain.

#### 4.1. BA 44 and hierarchical structure processing

Many theorists have suggested that the hierarchical nature of linguistic structures finds a correlation with the hierarchical nature of motor planning (e.g., Allott, 1994; Kimura, 1993; Lashley, 1951; Lieberman, 1984; MacNeilage, 1998). The present proposal states that the neural underpinning of the manipulation of these hierarchical structures is BA44.

Greenfield (1991, 1998) argues that young children's developing skills in the manipulation of hierarchically organized objects (e.g. cup nesting skills and tool use, such as using a spoon) precede their language development and serve as a preadaptation for it. Greenfield claims that there are three distinct developmental stages in children's 'Action Grammar', from the simplest Pairing strategy, then the Pot strategy, and finally the most complex Subassembly strategy. Fujita (2009) suggests that these strategies neatly correspond to the development of syntactic structures, in particular to the different modes of the application of the core syntactic operation 'Merge'.

BA44 is unique in connecting BA6 and BA45. BA44 connects the (phylogenetically ancient) motor-controlling BA6 and BA45, with the latter often claimed to be 'specifically linguistic' and of recent evolutionary vintage (see the review in Yusa, 2012; see also Fitch, 2011). Furthermore, an overlap of brain activity between tasks linked to language and tool use in the dorsal part of BA44 has been found (Higuchi, Chaminade, Imamizu, & Kawato, 2009), suggesting that similar neural structures are related to both language perception and tool use skills. The overlap of activities associated to the application of sequentially organized rules, that is 'action grammar', and comprehension of complex sentences supports our hypothesis that the same neural structures (BA44) devoted to hierarchical structure processing regardless of the cognitive domain. BA44 has indeed been suggested as the neural substrate for Greenfield's Action Grammar, and its lesion is responsible for problems with hierarchically organizing other people's behavior and understanding their intention. An association between BA 44 and the manipulation and selection of hierarchical syntactic structures (i.e. the selection and maintenance in working memory of hierarchically structured elements) is therefore quite plausible. As a matter of fact, numerous authors have already argued in favor of taking Broca's area as a 'supra-modal', non-linguistic specific hierarchical processor: Tettamanti and Weniger (2006), Koehlin and Jubault (2006), Fiebach and Schubotz (2006), Bahlmann, Schubotz, Mueller, Koester, and Friederici (2009),

Petersson et al. (2012), Wakita (2014), and Fitch and Martins (2014), offer evidence from the domains of music, action, and visuo-spatial processing.

The selection and maintenance in working memory of hierarchically structured elements that we attribute to BA44 corresponds to the first, Immobilization step of the linearization algorithm in Table 1. Viewed in this way, BA44 is akin to a memory buffer (the “abstract scratchpad” of Fitch & Martins, 2014), where successive ‘snapshots’ of the processing of hierarchical structures can be offloaded, and later retrieved.

Concerning the temporal regions to which BA44 connects, it should be noted that many details concerning the precise function of these areas remain unclear. However, Lohmann et al. (2010) observe that the posterior portion of the left STS was consistently activated in a range of language experiments. Specifically, the left posterior STS/STG has been discussed to support the processing of syntactic, verb argument, and prosodic information (Bornkessel et al., 2005; Brauer & Friederici, 2007; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Humphries, Love, Swinney, & Hickok, 2005); for a review, see Vigneau et al. (2006). As Lohmann et al. (2010) note, these findings have led to the interpretation of the left posterior STS/STG as a region supporting the integration of different information types during perception (Friederici, 2002; Grewe et al., 2007) or as an auditory–motor interface (Hickok & Poeppel, 2007).

In the context of our proposal, the fact that the left posterior STS/STG has been related to the processing of information above the lexical level, such as “syntactic, verb argument, and prosodic information” is highly relevant, as this is the sort of information that we expect to be related to the first stage of linearization.

In sum, the BA44/temporal connection via the dorsal pathway would provide a storage mechanism that essentially amounts to the role of the stack in a pushdown automaton (in this we are in agreement with Fitch & Martins, 2014).

#### 4.2. BA 45 and Vocabulary Insertion

BA45/the pars triangularis, has been shown to be involved in several language-specific tasks. More concretely, this specific region is activated in semantic tasks (Bookheimer, 2002; Fiez, 1997; Hagoort, 2005; Hagoort, Hald, Bastiaansen, & Petersson, 2004; Poldrack et al., 1999; Rodd, Davis, & Johnsrude, 2005; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Thompson-Schill, Aguirre, D’Esposito, & Farah, 1999; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000).

As it has been previously noted, BA45 shows evolutionarily newer characteristics compared to BA44 (Fitch, 2011; Yusa, 2012). This is expected under our hypothesis, given that BA45 manipulates objects that are more domain-specific than those dealt with by BA44: there is nothing more linguistically specific than vocabulary items: units that combine syntactic, semantic, and phonological information. They are the perfect illustration of the operation Unify (Hagoort, 2005; Jackendoff, 2002). This is not to say that this function has no evolutionary precursors. Other animals are certainly able to form meaning-sound pairs (‘proto-words’), for which BA45 is plausibly involved. But the addition of syntactic structuring in the course of evolution certainly led to an enhancement of the roles BA45 may have had in our ancestors—an enhancement that we expect to see reflected at the cytoarchitectonic level as well as at the connectivity level.

Interestingly, BA45 connects ventrally to the temporal lobe, and as such is related to the “ventral” stream system (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982), a memory-based system, which has been claimed to underlie the formation of perceptual representations of objects and their relations (Goodale, 2000). Parts of BA 45 also connect to BA47, which several authors have linked to aspects of semantic expectation (Sabb, Bilder, Chou, & Bookheimer, 2007; de Zubicaray & McMahon, 2009). BA 47/pars orbitalis, together with the temporal pole, are claimed to be “[i]nvolved in the binding of syntactic structures with lexico-semantic representations” (Monzalvo & Dehaene-Lambertz, 2013, p. 364; see also Dapretto & Bookheimer, 1999; Pallier, Devauchelle, & Dehaene, 2011; Price, 2010). Fiebach, Friederici, Mueller, and von Cramon (2002) also implicate BA45 in lexical selection.

Additional evidence for our hypothesis may come from language impairment studies. Evidence from individuals with Primary Progressive Aphasia (PPA) recently assessed in Galantucci et al. (2011) show how distinct dorsal and ventral pathways in the brain may subserve different linearization



sub-operations. Comparing all three PPA variants, different connectivity patterns for each PPA variant have been found. More precisely, in non-fluent/agrammatic individuals, the ventral tract is found to be spared while the dorsal tract is damaged. Concretely, Galantucci et al. (2011) pointed out that in their nonfluent PPA individuals, changes in DTI metrics were found predominantly “[i]n the left dorsal language pathways connecting frontoparietal or frontotemporal regions, but not in ventral tracts connecting the temporal lobe to the occipital lobe or to the orbitofrontal cortex” (Galantucci et al., 2011, p. 8). In the same vein, according to Wilson et al. (2011) study on white matter damage and syntactic deficits in 27 primary progressive aphasics, their findings suggest that syntactic processing depends mainly on dorsal tracts, since there is a “[s]trong correlation between reduced FA in the SLF/Arcuate and deficits in syntactic comprehension and production.”

White matter ventral tracts are most severely affected in semantic variant PPA patients. Precisely this group show predominantly profound lexical deficits encompassing lexical retrieval, single word comprehension, and semantic knowledge (e.g. Galantucci et al., 2011; Gorno-Tempini et al., 2004; Hodges & Patterson, 1996), but spared syntactic processing. Wilson et al. (2011) findings also lead to the same direction. Interestingly enough, damage to ventral tracts – the ECFS or the UF – does not seem to result in syntactic deficits in PPA population (Wilson et al., 2011). Their results reinforce the claim that damage to the ventral tracts is not associated with syntactic deficits, showing that syntactic processing depends primarily on dorsal pathways and, as they pointed out, “[t]he role of ventral tracts in single word processing is consistent with the observation that regions connected by ventral tracts are activated by language comprehension (Saur et al., 2008), since language comprehension typically involves both lexical and syntactic processes” (Wilson et al., 2011, p. 401). These findings seem to delineate a particular role of the ventral pathway in language processing, showing its importance in lexical processing at the single word level.

In the context of the ventral stream to which BA45 belongs, it is interesting to note that numerous authors have offered evidence for an anterior processing gradient within the temporal cortex, a semantic memory storage for units ranging from phonemes to words and on to phrases (see Bornkessel-Schlesewsky & Schlesewsky, 2013; DeWitt & Rauschecker, 2012; Westerlund & Pykkänen, 2014). Thus, part of the temporal lobe appears to be ideally suited to offer memorized structural templates of various sizes that obviously match the elements that emerge in the course of the linearization process, particularly step 2, where lexico-semantic considerations come into play.

#### 4.3. Additional considerations: the frontal operculum and sub-cortical structures

Building on Friederici’s claim (Friederici et al., 2003; Friederici, Bahlmann, Heim, Shubotz, & Anwander, 2006) that the FO is dedicated to more local operations, of the finite state/linear adjacency kind, we are tempted to ascribe the third sub-operation of linearization to that part of Broca’s area. Like, BA 6, the deep frontal operculum is “agranular”: it lacks any distinct layer 4—a trait typical of motor regions. It therefore makes sense to relate this brain structure to the tail end of the linearization process.

Several studies appear to confirm our hypothesis. Fiebach and Schubotz (2006), Price et al. (2003), Fiez and Petersen (1998), Mechelli et al. (2005), and Cattinelli (2010) all attribute a phonological role to the operculum (e.g., “sublexical phonological decisions”, “manipulations of phonological representations”, “phonological output processes”).

Although we are mindful of the limitations of Artificial Grammar learning experiments, well illustrated in Petersson et al.’s (2012) excellent review, we think that Friederici’s claim that the Frontal Operculum is associated with the establishment and maintenance of more local dependencies (for us, the Serialization operation), which relies on Artificial Grammar-based experiments, makes sense in light of the fact that the frontal operculum is part of a phylogenetically ancient network known to be involved in the computation of finite-state grammars (see Fitch & Martins, 2014 for review).

We hasten to add that in addition to cortical structures such as Broca’s region, sub-cortical structures, in particular, the basal ganglia, the thalamus and the cerebellum are likely to play a significant role in the manipulation, selection, and serialization of linguistic objects (Chan, Ryan, & Bever, 2013; Ullman, 2004). Indeed, the basal ganglia have been associated to several cognitive functions, including sequence learning (Aldridge & Berridge, 1998; Boecker et al., 1998; Chan, 2007; Doyon et al., 1997; Graybiel, 1995; Peigneux et al., 2000; Willingham, 1998); real-time motor planning and control

(Wise et al., 1996), and processes involving the precise timing (Penhune, Zatorre, & Evans, 1998) and the selection or switching among multiple motor programs (Haaland, Harrington, O'Brien, & Hermanowicz, 1997); interval timing and rhythm (Meck & Benson, 2002; Schubotz & von Cramon, 2001); and context-dependent rule-based selection (Peigneux et al., 2000; Wise et al., 1996). The study by Jin, Fujii, and Graybiel (2009) on the representation of time in the basal ganglia is perhaps the most explicit in this respect.

The basal ganglia are thus implicated in aspects of selection or real-time shifting of representations. As Ullman (2005) suggests, the basal ganglia are poised to play an important role in one or more aspects of the real-time selection and maintenance in working memory of (and switching between) sequentially and hierarchically structured elements in complex linguistic representations, and should therefore figure in any hypothesis like the present one that seeks to shed light on how serial order is computed.

In related work, Miller and Buschman (2007) argue that cortico-striatal loops underlie the ability to learn temporal sequences of patterns. Such loops may find a 'computational correlate' in the matching of tree structures with stored lexical entries in models like Bye and Svenonius (2012). As a matter of fact, the model put forth by Miller and Buschman strikes us as perfectly designed for encoding the parametric dependencies attributed to lexical items (and not to syntax) by theoretical linguists (see Boeckx & Leivada, 2013).

In addition to the basal ganglia, the thalamus may also play a role, based on experimental evidence that it is involved in lexical semantic decision tasks (Pergola et al., 2013; de Witte, Wilssens, Engelborghs, De Deyn, & Mariën, 2006). Likewise, as reviewed in Wijnen (2013), the cerebellum is an important component of the brain involved in the neurocognition of sequential learning. Thus, in addition to the cortical subregions and pathways discussed in this article, we believe that a complete picture of the functional neuroanatomy of serial order will have to take the basal ganglia, the cerebellum, and the thalamus into account.

## 5. The broader picture

Although our hypothesis was inspired by Friederici's research program of mapping aspects of grammar onto a finer picture of the brain, there are several differences between our and Friederici's proposals. These are worth highlighting, as they enable us to make connections with the proposal put forth in Bornkessel-Schlesewsky and Schlewsky (2013), which is also critical of Friederici's specific claims, and which we think is closer to the model we envisage.

To begin with, we agree with Bornkessel-Schlesewsky and Schlewsky in taking the frontal cortex (for us, specifically, Broca's region) not to be responsible for 'syntax' (see also, Petersson et al., 2012). For Bornkessel-Schlesewsky and Schlewsky, the frontal cortex does not subservise linguistic processing functions. In fact, they propose that linguistic processing per se only takes place in the temporal and parietal regions (a claim which relates to the connection we have established between the operation of immobilization of syntactic structures and the dorsal pathway). Frontal cortex, for them, subserves control functions only and serves to link linguistic processing to behavior. Moreover, it serves to integrate information from the ventral and dorsal streams and to provide top-down feedback information to each stream. This converges with our view that Broca's region is involved in the mapping from syntax to linear strings (and ultimately, to the externalization of abstract linguistic structures), and is critical in selecting and unifying different types of information (syntactic, semantic, and phonological).

This is a significant departure from Friederici's model, where syntax is crucially tied to Broca's regions. In the latest version of Friederici's account (Friederici, 2012), BA44 is described as playing "a particular role in creating argument hierarchies as a sentence is computed" and as the "core syntax region" (Friederici, 2012, p. 265). In addition, for Friederici, different subregions of Broca's area are responsible for different 'kinds' of 'syntax'. For example, for her, the dorsal stream (more precisely, dorsal pathway II) only comes into play during the comprehension of syntactically complex sentences, that is, sentences involving either clausal embedding or deviations from the basic word order. But as Bornkessel-Schlesewsky and Schlewsky (2013) correctly observe, syntactic mechanisms are identical between "simple" and "complex" sentences (i.e. complex sentences may involve an increased number of applications of these operations, but not the application of qualitatively different principles). Thus,

there is no theoretical linguistic basis for the dichotomy between simple and complex syntax that is an important component of Friederici's model, and an argument for decomposing Broca's area. We think that Bornkessel-Schlesewsky and Schlesewsky are right in not viewing complexity of the sentences in question as a prerequisite for the involvement of the dorsal stream.

For Bornkessel-Schlesewsky and Schlesewsky, the phenomena summarized by Friederici (2009) under the label "hierarchical syntax" are more parsimoniously explained in terms of a gradient of cognitive control in prefrontal cortex in the sense of Koechlin and colleagues (Koechlin, Ody, & Kouneiher, 2003; Koechlin & Summerfield, 2007). Bornkessel-Schlesewsky and Schlesewsky take the dorsal versus ventral distinction as meaningful at a functional level. That is, like us and many other authors, they assume that there are differences in the type(s) of information transferred along each stream and/or in the mechanisms of information processing. For them, the streams serve separable functions of information processing and a unifying function can be defined for each stream, irrespective of the possible presence of multiple anatomical subpathways. Both the dorsal and ventral streams have the function of combining elements/features to form successively more complex representations, but the nature of these representations differs fundamentally for each stream, in a way that is compatible with our proposal.

For Bornkessel-Schlesewsky and Schlesewsky, the ventral stream performs time-independent unifications of conceptual schemata, serving to create auditory objects of increasing complexity, whereas the dorsal stream engages in the time-dependent combination of elements, subserving both syntactic structuring and a linkage to action. Time-dependent processing is typically associated with the dorsal stream, e.g. in terms of "encoding and storing sound sequences" (Scott & Wise, 2004, p. 27) or in supporting working memory (Saur et al., 2008). The ventral stream, by contrast, is viewed as more time-independent in most approaches discussed by Bornkessel-Schlesewsky and Schlesewsky, which fits well with our proposal that ties the ventral stream to time-invariant semantic representations.

In Bornkessel-Schlesewsky and Schlesewsky's own words,

"[t]he function of the ventral stream lies in the time-independent identification and unification of conceptual schemata, serving to represent conceptual chunks of increasing size. [...] The function of the dorsal stream lies in the identification and combination of successively larger linguistic chunks in time. This comprises the prosodic segmentation of the input and the subsequent combination of elements into category sequences. In addition, it involves the computation of all time-dependent sentence internal relations (e.g. computing which participant is the actor, i.e. the participant primarily responsible for the state of affairs described)" (p. 67).

Like us, Bornkessel-Schlesewsky and Schlesewsky see Broca's region as crucially involved in selection among alternative representations. As they write, a number of scholars have argued that Broca's region is engaged in processes of cognitive control during language processing, rather than in linguistic computation per se (e.g. Stowe, Haverkort, & Zwarts, 2005; Stowe et al., 1998; Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill et al., 1997). These arguments have been extended specifically to syntax in studies demonstrating an increase of Left Inferior Frontal Gyrus activation for sentences involving ambiguity and, hence, an increased need to select among competing alternatives (Novick, Trueswell, & Thompson-Schill, 2005). This activation overlaps with activation elicited in a classic cognitive control paradigm (the Stroop task; January, Trueswell, & Thompson-Schill, 2009).

Under this perspective, just as in our proposal, the parts of Broca's region connected to the dorsal stream are closer to syntax, whereas the parts connected to the ventral stream are connected to semantics (the terms 'syntax' and 'semantics' are used here somewhat loosely; we do not mean to suggest that these are monolithic processes). Bornkessel-Schlesewsky and Schlesewsky indeed observe that the ventral stream has been proposed as a stream for extracting semantics in language understanding (e.g. Saur et al., 2008; Scott, Blank, Rosen, & Wise, 2000; Ueno, Saito, Rogers, & Lambon Ralph, 2011; and, to a certain degree, Hickok & Poeppel, 2007). Specifically, the representations dealt with in the ventral stream for Bornkessel-Schlesewsky and Schlesewsky are complete word-level semantic representations. The key process for these is the form-to-meaning mapping at the word level, thus explaining the findings by Saur et al. (2008), DeWitt and Rauschecker (2012) and the results on semantic dementia (Ueno et al., 2011).

Bornkessel-Schlesewsky and Schlesewsky's model converges to some extent with Saur et al. (2008), who link the dorsal stream in language comprehension to working memory: "involvement of the dorsal stream for processing of complex syntactic operations might be partially explained as a result of an increase in syntactic working memory load" (Saur et al., 2008, p. 18039). (On the role of BA44 and working memory in 'syntax', see also Chesi & Moro, 2014.) But we think that Bornkessel-Schlesewsky and Schlesewsky are right in stressing that working memory is always required when a sequence of more than two elements is processed in time (in other words, this is not a return of Friederici's notion of complex syntax).

## 6. Conclusion

Linguistically, it is worth emphasizing that the different linguistic domains such as syntax, semantics, or phonology are not monolithic domains characterized by a single computation. Rather, they consist of different operations that are not necessarily language-specific per se. But even 'single' operations like linearization are not monolithic. Nor are they necessarily exclusively linguistic in nature. After all, the Idsardi and Raimy model we have exploited here rests on generic operations: despite their domain-specific formulations in the literature, both Immobilization and Vocabulary Insertion boil down to the selection of representations, the binding of features (unification), and the association of units with timing slots. There is nothing uniquely linguistic about these, other than the specific representations involved. These may be unified in Broca's region, but their constructions likely involve other networks, as a growing number of authors anticipate (Boeckx & Benítez-Burraco, 2014; Bornkessel-Schlesewsky & Schlesewsky, 2013; Fedorenko & Thompson-Schill, 2014; Petersson et al., 2012).

Our main point is that without decomposing formal operations like linearization we would not be able to relate them to what our current knowledge about the functional anatomy of the brain suggests. At the same time, failure to decompose standard areas like Broca's region would make it difficult to map formal operations onto brain junctures. In sum, parallel decomposition appears to be required to arrive at the relevant level of granularity at which one can begin to formulate (and subsequently test) linking hypotheses between formal linguistic theory and neuroscience.

We hope that the linking hypothesis argued for in this paper will be put to the test in future experimental work. The theoretical literature on which we have relied to decompose the linearization process already offers a rich data set on which to draw to design experiments that may well be able to detect brain activity changes at the junctures we have hypothesized here when violations occur as syntactic structures are mapped onto linear strings.

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## References

- Aldridge, J. W., & Berridge, K. C. (1998). Coding of serial order by neostriatal neurons: a 'natural action' approach to movement sequence. *Journal of Neuroscience*, 18(7), 2777–2787.
- Allott, R. M. (1994). Motor theory of language origin: the diversity of languages. In J. Wind, A. Jonker, R. M. Allott, & L. Rolfe (Eds.), *Studies in language origins* (pp. 125–160). Amsterdam: John Benjamins.
- Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., et al. (2010). Broca's region: novel organization principles and multiple receptor mapping. *PLoS Biology*, 8(9), 1–16.
- Anwander, A., Tittgemeyer, M., Von Cramon, D. Y., Friederici, A. D., & Knosche, T. R. (2007). Connectivity-based parcellation of Broca's area. *Cerebral Cortex*, 17, 816–825.
- Arregi, K., & Nevins, A. I. (2012). *Morphotactics: Basque auxiliaries and the structure of spell-out*. Dordrecht: Springer.
- Bahlmann, J., Schubotz, R. I., Mueller, J. L., Koester, D., & Friederici, A. D. (2009). Neural circuits of hierarchical visuo-spatial sequence processing. *Brain Research*, 1298, 161–170.
- Boecker, H., Dagher, A., Ceballos-Baumann, A. O., Passingham, R. E., Samuel, M., Friston, K. J., et al. (1998). Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: investigations with H2 15O PET. *Journal of Neurophysiology*, 79(2), 1070–1080.

- Boeckx, C. (2014). *Elementary syntactic structures*. Cambridge: Cambridge University Press.
- Boeckx, C., & Benítez-Burraco, A. (2014). The shape of the human language-ready brain. *Frontiers in Psychology*, 5. <http://dx.doi.org/10.3389/fpsyg.2014.00282>.
- Boeckx, C., & Leivada, E. (2013). Entangled parametric hierarchies: problems for an overspecified universal grammar. *PLoS ONE*, 8(9), e72357.
- Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, 25, 151–188.
- Bornkessel, I., Zysset, S., von Cramon, D. Y., Friederici, A. D., & Schlesewsky, M. (2005). Who did what to whom? The neural basis of argument hierarchies during language comprehension. *NeuroImage*, 26, 221–233.
- Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: a new dorsal–ventral stream model of sentence comprehension. *Brain and Language*, 125, 60–76.
- Brauer, J., & Friederici, A. D. (2007). Functional neural networks of semantic and syntactic processes in the developing brain. *Journal of Cognitive Neuroscience*, 19, 1609–1623.
- Bye, P., & Svenonius, P. (2012). Non-concatenative morphology as epiphenomenon. In J. Trommer (Ed.), *The morphology and phonology of exponence* (pp. 427–495). Oxford: Oxford University Press.
- Cattinelli, I. (2010). *Investigations on cognitive computation and computational cognition* (PhD dissertation). Università Degli Studi di Milano.
- Chan, S. (2007). *Linguistic sequencing in the cortex and basal ganglia* (PhD dissertation). The University of Arizona.
- Chan, S., Ryan, L., & Bever, T. (2013). Role of the striatum in language: syntactic and conceptual sequencing. *Brain and Language*, 125, 283–294.
- Chesi, C., & Moro, A. (2014). Computational complexity in the brain. In F. J. Newmeyer, & L. B. Preston (Eds.), *Measuring linguistic complexity*. Oxford: Oxford University Press.
- Chomsky, N. (1957). *Syntactic structures*. The Hague/Paris: Mouton.
- Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron*, 24(2), 427–432.
- DeWitt, L., & Rauschecker, J. P. (2012). Phoneme and word recognition in the auditory ventral stream. *Proceedings of the National Academy of Sciences of the United States of America*, 109(8), E505–E514.
- Doyon, J., Gaudreau, D., Laforce, R., Jr., Castonguay, M., Bedard, P. J., Bedard, F., et al. (1997). Role of the striatum, cerebellum, and frontal lobes in the learning of a visuomotor sequence. *Brain and Cognition*, 34(2), 218–245.
- Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology*, 22, 2059–2062.
- Fedorenko, E., & Thompson-Schill, S. L. (2014). Reworking the language network. *Trends in Cognitive Science*, 18(3), 120–126.
- Fiebach, C. J., Friederici, A. D., Mueller, K., & von Cramon, D. Y. (2002). fMRI evidence for dual routes to the mental lexicon in visual word recognition. *Journal of Cognitive Neuroscience*, 14(1), 11–23.
- Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: a common role for Broca's area and ventral premotor cortex across domains? *Cortex*, 42(4), 499–502.
- Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping*, 5, 79–83.
- Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 914–921.
- Fitch, W. T. (2011). The evolution of syntax: an exaptationist perspective. *Frontiers in Evolutionary Neuroscience*, 3(9), 1–12.
- Fitch, W. T., & Martins, M. D. (2014). Hierarchical processing in music, language, and action: Lashley revisited. *Annals of the New York Academy of Sciences*. <http://dx.doi.org/10.1111/nyas.12406>.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Science*, 6, 78–84.
- Friederici, A. D. (2009). Pathways to language: fiber tracts in the human brain. *Trends in Cognitive Science*, 4, 175–181.
- Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiological Reviews*, 91, 1357–1392.
- Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Science*, 5, 262–268.
- Friederici, A. D., Bahlmann, J., Heim, S., Shubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 2458–2463.
- Friederici, A. D., Rüschemeyer, S. A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral Cortex*, 13(2), 170–177.
- Fujita, K. (2009). A prospect for evolutionary adequacy: merge and the evolution and development of human language. *Bio-linguistics*, 3(2), 128–153.
- Galantucci, S., Tartaglia, M. C., Wilson, S. M., Henry, M. L., Filippi, M., Agosta, F., et al. (2011). White matter damage in primary progressive aphasia: a diffusion tensor tractography study. *Brain*, 134. <http://dx.doi.org/10.1093/brain/awr099>.
- Goodale, M. A. (2000). Perception and action in the human visual system. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 365–378). Cambridge, MA: MIT Press.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Gorno-Tempini, M. L., Dronkers, N. F., Rankin, K. P., Ogar, J. M., Phengrasamy, L., Rosen, J. H., et al. (2004). Cognition and anatomy in three variants of primary progressive aphasia. *Annals of Neurology*, 55, 335–346.
- Graybiel, A. (1995). The basal ganglia. *Trends in Neurosciences*, 18, 60–62.
- Greenfield, P. M. (1991). Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, 14, 531–595.
- Greenfield, P. M. (1998). Language, tools, and brain revisited. *Behavioral and Brain Sciences*, 21(1), 159–163.
- Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2006). Linguistic prominence and Broca's area: the influence of animacy as a linearization principle. *NeuroImage*, 32(3), 1395–1402.
- Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2007). The role of the posterior superior temporal sulcus in the processing of unmarked transitivity. *NeuroImage*, 35(1), 343–352.
- Haaland, K. Y., Harrington, D. L., O'Brien, S., & Hermanowicz, N. (1997). Cognitive-motor learning in Parkinson's disease. *Neuropsychology*, 11(2), 180–186.

- Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Science*, 9, 416–423.
- Hagoort, P., Hald, L., Bastiaansen, M., & Petersson, K. M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science*, 304(5669), 438–441.
- Halle, M., & Marantz, A. (1993). Distributed morphology and the pieces of inflection. In K. Hale, & S. J. Keyser (Eds.), *The view from building 20* (pp. 111–176). Cambridge, MA: MIT Press.
- Harley, H., & Noyer, R. (2003). Distributed morphology. In L. Cheng, & R. Sybesma (Eds.), *The second Glot International state-of-the-article book* (pp. 463–496). Berlin: Mouton de Gruyter.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8, 393–402.
- Higuchi, S., Chaminade, T., Imamizu, H., & Kawato, M. (2009). Shared neural correlates for language and tool use in Broca's area. *Cognitive Neuroscience and Neuropsychology*, 20, 1376–1381.
- Hodges, J. R., & Patterson, K. (1996). Nonfluent progressive aphasia and semantic dementia: a comparative neuropsychological study. *Journal of the International Neuropsychological Society*, 2, 511–524.
- Hornstein, N. (2009). *A theory of syntax*. Cambridge: Cambridge University Press.
- Humphries, C., Love, T., Swinney, D., & Hickok, G. (2005). Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Human Brain Mapping*, 26, 128–138.
- Idsardi, W. J., & Raimy, E. (2013). Three types of linearization and the temporal aspects of speech. In M. T. Biberauer, & I. Roberts (Eds.), *Challenges to linearization* (pp. 31–56). Berlin: Mouton de Gruyter.
- Jackendoff, R. (2002). *Foundations of language: Brain, meaning, grammar, evolution*. Oxford: Oxford University Press.
- January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of Stroop and syntactic ambiguity resolution in Broca's area: implications for the neural basis of sentence processing. *Journal of Cognitive Neuroscience*, 21, 2434–2444.
- Jin, D. Z., Fujii, N., & Graybiel, A. M. (2009). Neural representation of time in cortico-basal ganglia circuits. *Proceedings of the National Academy of Sciences of the United States of America*, 106(45), 19156–19161.
- Kayne, R. S. (1994). *The antisymmetry of syntax*. Cambridge, MA: MIT Press.
- Kimura, D. (1993). *Neuromotor mechanisms in human communication*. Oxford: Oxford University Press.
- Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron*, 50, 963–974.
- Koechlin, E., Ody, C., & Kouneither, F. (2003). The architecture of cognitive control in the human prefrontal cortex. *Science*, 302, 1181–1185.
- Koechlin, E., & Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends in Cognitive Sciences*, 11, 229–235.
- Lashley, K. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior* (pp. 112–146). New York: Wiley.
- Lieberman, P. (1984). *The biology and evolution of language*. Cambridge, MA: Harvard University Press.
- Lohmann, G., Hoehl, S., Brauer, J., Danielmeier, C., Bornkessel-Schlesewsky, I., Bahlmann, J., et al. (2010). Setting the frame: the human brain activates a basic low-frequency network for language processing. *Cerebral Cortex*, 20(6), 1286–1292.
- MacNeilage, P. F. (1998). The frame/content theory of evolution of speech production. *Journal of Behavioral Brain Science*, 21, 499–546.
- Marr, D. (1982). *Vision*. San Francisco, CA: Freeman.
- Mechelli, A., Crinion, J. T., Long, S., Friston, K. J., Lambon Ralph, M. A., Patterson, K., et al. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of Cognitive Neuroscience*, 17(11), 1753–1765.
- Meck, W. H., & Benson, A. M. (2002). Dissecting the brain's internal clock: how frontal-striatal circuitry keeps time and shifts attention. *Brain and Cognition*, 48, 195–211.
- Miller, E. K., & Buschman, T. J. (2007). Rules through recursion: how interactions between the frontal cortex and basal ganglia may build abstract, complex rules from concrete, simple ones. In S. A. Bunge, & J. D. Wallis (Eds.), *Neuroscience of rule-guided behavior* (pp. 419–440). New York: Oxford University Press.
- Monzalvo, K., & Dehaene-Lambertz, G. (2013). How reading acquisition changes children's spoken language network. *Brain & Language*, 127, 356–365.
- Neubert, F. X., Mars, R. B., Thomas, A. G., Sallet, J., & Rushworth, M. F. (2014). Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex. *Neuron*, 81(3), 700–713.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective and Behavioral Neuroscience*, 5, 263–281.
- Pallier, C., Devauchelle, A. D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences of the United States of America*, 108(6), 2522–2527.
- Peigneux, P., Maquet, P., Meulemans, T., Destrebecqz, A., Laureys, S., Degueldre, C., et al. (2000). Striatum forever despite sequence learning variability: a random effect analysis of PET data. *Human Brain Mapping*, 10, 179–194.
- Penhune, V. B., Zatorre, R. J., & Evans, A. C. (1998). Cerebellar contributions to motor timing: a PET study of auditory and visual rhythm reproduction. *Journal of Cognitive Neuroscience*, 10(6), 752–765.
- Pergola, G., Bellebaum, C., Gehlhaar, B., Koch, B., Schwarz, M., Daum, I., et al. (2013). The involvement of the thalamus in semantic retrieval: a clinical group study. *Journal of Cognitive Neuroscience*, 25, 872–886.
- Petersson, K. M., Folia, V., & Hagoort, P. (2012). What artificial grammar learning reveals about the neurobiology of syntax. *Brain and Language*, 120, 83–95.
- Pfau, R. (2009). *Grammar as processor: A distributed morphology account of spontaneous speech errors*. Amsterdam: John Benjamins.
- Poeppel, D. (2005). The interdisciplinary study of language and its challenges. In D. Grimm (Ed.), *Jahrbuch des Wissenschaftskollegs zu Berlin*. Germany.
- Poeppel, D. (2011). Genetics and language: a neurobiological perspective on the missing link(-ing hypotheses). *Journal of Neurodevelopmental Disorders*, 3, 381–387.
- Poeppel, D. (2012). The maps problem and the mapping problem: two challenges for a cognitive neuroscience of speech and language. *Cognitive Neuropsychology*, 29(1–2), 34–55.
- Poeppel, D., & Embick, D. (2005). The relation between linguistics and neuroscience. In A. Cutler (Ed.), *Twenty-first century psycholinguistics: Four cornerstones* (pp. 173–189). London: Lawrence Erlbaum.

- Poldrack, R. A., Wagner, A. D., Prull, M., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage*, *10*, 15–35.
- Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, *1191*(1), 62–88.
- Price, C. J., Gorno-Tempini, M. L., Graham, K. S., Biggio, N., Mechelli, A., Patterson, K., et al. (2003). Normal and pathological reading: converging data from lesion and imaging studies. *NeuroImage*, *20*, S30–S41.
- Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex*, *15*, 1261–1269.
- Rogalsky, C., & Hickok, G. (2011). The role of Broca's area in sentence comprehension. *Journal of Cognitive Neuroscience*, *23*(7), 1664–1680.
- Sabb, F. W., Bilder, R. M., Chou, M., & Bookheimer, S. Y. (2007). Working memory effects on semantic processing: priming differences in pars orbitalis. *NeuroImage*, *37*, 311–322.
- Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M. S., et al. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 18035–18040.
- Schubotz, R. I., & von Cramon, D. Y. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cerebral Cortex*, *11*, 210–222.
- Scott, S., Blank, C., Rosen, S., & Wise, R. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain*, *123*, 2400–2406.
- Scott, S. K., & Wise, R. J. S. (2004). The functional neuroanatomy of prelexical processing in speech perception. *Cognition*, *92*, 13–45.
- Stowe, L. A., Broere, C., Paans, A., Wijers, A., Mulder, G., Vaalburg, W., et al. (1998). Localising components of a complex task: sentence processing and working memory. *Neuroreport*, *9*, 2995–2999.
- Stowe, L. A., Haverkort, M., & Zwarts, F. (2005). Rethinking the neurological basis of language. *Lingua*, *115*, 997–1042.
- Tettamanti, M., & Weniger, D. (2006). Broca's area: a supramodal hierarchical processor? *Cortex*, *42*, 491–494.
- Thompson-Schill, S. L., Aguirre, G. K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, *37*, 671–676.
- Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*, 219–224.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left prefrontal cortex in retrieval of semantic knowledge: a re-evaluation. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 14792–14797.
- Ueno, T., Saito, S., Rogers, T. T., & Lambon Ralph, M. A. (2011). Lichtheim 2: synthesizing aphasia and the neural basis of language in a neurocomputational model of the dual dorsal–ventral language pathways. *Neuron*, *72*, 385–396.
- Ullman, M. T. (2004). Contributions of memory circuits to language: the declarative/procedural model. *Cognition*, *92*, 231–270.
- Ullman, M. T. (2005). A cognitive neuroscience perspective on second language acquisition: the declarative/procedural model. In C. Sanz (Ed.), *Mind and context in adult second language acquisition: Methods, theory, and practice* (pp. 141–178). Washington, DC: Georgetown University Press.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Vigneau, M., Beaucousin, V., Herve, P., Duffau, H., Crivello, F., Houde, O., et al. (2006). Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *NeuroImage*, *30*, 1414–1432.
- de Vries, M. (2009). On multidominance and linearization. *Biolinguistics*, *3*(4), 344–403.
- Wagner, A. D., Koutstaal, W., Maril, A., Schacter, D. L., & Buckner, R. L. (2000). Task-specific repetition priming in left inferior prefrontal cortex. *Cerebral Cortex*, *10*, 1176–1184.
- Wakita, M. (2014). Broca's area processes the hierarchical organization of observed action. *Frontiers in Human Neuroscience*, *17*(7), 937.
- Westerlund, M., & Pyllkkänen, L. (2014). The role of the left anterior lobe in semantic composition vs. semantic memory. *Neuropsychologia*, *57*, 59–70.
- Wijnen, F. (2013). Acquisition of linguistic categories: cross-domain convergence. In J. Bolhuis, & M. Everaert (Eds.), *Birdsong, speech, and language: Exploring the evolution of mind and brain* (pp. 157–177). Cambridge, MA: MIT Press.
- Willingham, D. B. (1998). A neuropsychological theory of motor skill learning. *Psychological Review*, *105*(3), 558–584.
- Wilson, S. M., Galantucci, S., Tartaglia, M. C., Rising, K., Patterson, D. K., Henry, M. L., et al. (2011). Syntactic processing depends on dorsal language tracts. *Neuron*, *72*, 397–403.
- Wise, S. P., Fried, I., Olivier, A., Paus, T., Rizzolatti, G., & Zilles, K. J. (1996). Workshop on the anatomic definition, boundaries of the supplementary sensorimotor area. *Advances in Neurology*, *70*, 489–495.
- de Witte, L., Wilssens, I., Engelborghs, S., De Deyn, P. P., & Mariën, P. (2006). Impairment of syntax and lexical semantics in a patient with bilateral paramedian thalamic infarction. *Brain and Language*, *96*, 69–77.
- Yusa, N. (2012). Structure dependence in the brain. In L. McCrohon, T. Fujimura, K. Fujita, R. Martin, K. Okanoya, R. Suzuki, et al. (Eds.), *Five approaches to language evolution. Proceedings of the workshops of the 9th international conference on the evolution of language* (pp. 25–26). Kyoto: Evolang9 Organizing Committee.
- Zilles, K., & Amunts, K. (2009). Receptor mapping: architecture of the human cerebral cortex. *Current Opinion in Neurology*, *22*, 331–339.
- de Zubicaray, G. I., & McMahon, K. L. (2009). Auditory context effects in picture naming investigated with event-related fMRI. *Cognitive, Affective, & Behavioral Neuroscience*, *9*, 260–269.