A Companion to Chomsky

Edited by

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WILEY Blackwell

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Neuroscience and Syntax

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20.1   Introduction

The neuroscience of language studies the relationship between linguistic phenomena and the structure and functioning of the human brain. Neurolinguists combine insights from linguistic theory with experimental methodologies coming from cognitive neuroscience and biomedical research, to explore how language and the brain map onto each other at the neuroanatomical level. In this chapter, we focus on the neural basis supporting the remarkable human capacity to effortlessly assemble single words into more complex hierarchical structures, thus enabling the production and comprehension of unbounded arrays of different linguistic expressions.

A detailed characterization of the fundamentally hierarchical nature of human language has been already at the heart of linguistic theory since the advent of the generative enterprise in the second half of the previous century. A major objective within the generative framework has been to make humans' knowledge of grammar explicit, that is distinguishing grammatical from ungrammatical sequences by showing how relations between linear sequences of words (expressed as assemblies of sounds, characters, or signs) result from more abstract structural relations in the human mind. In this sense, linguistic expressions consist of hierarchical grouping relations which cannot be determined solely by the linear order of elements. Consider the sentence in (1), which can be represented either as a hierarchical tree in (2), or as a flat structure in (3):

(1)   The boy eats an apple

(2)

```
              S
        _____|_____
       |   |   |      |
       |   |   |     _|_
      the boy eats  |   |
                   an  apple
```

(3)

```
          S
       ___|___
      |       |
  the boy eats an apple
```
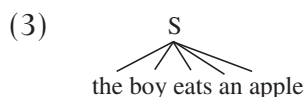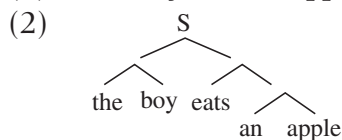
Empirical tests on tree structures like (2) and (3) exist, which can be used to assess the superiority of hierarchy over linearization, by showing that some sequences of words behave as units when certain syntactic manipulations are applied to the sentence (see "constituent analysis"; Harris 1946; Nida 1948; Pike 1943; Wells 1947). For example, a syntactic unit like *an apple* in (4) can be focus in a cleft construction in (5), while non-units, like *apple in* cannot in (6):

(4)   The boy eats an apple in the park
(5)   It is an apple that the boy eats __ in the park
(6)   *It is apple in that the boy eats an __ the park

The absence of any intermediate phrasal level between single words and the sentence node in (3) above would not be able to predict the possibility of dislocating units within the sentence, nor any asymmetry between (5) and (6). The discovery that certain relations (e.g., c-command; Reinhart 1976) regulate binding between distinct units in the sentence (e.g., anaphors and antecedents) according to pervasive structure-dependent principles has considerably strengthened the hierarchically-based hypothesis for language expressions.

Developments within the generative framework in the last decades have concentrated on the precise characterization of the mechanism enabling hierarchical structures to be generated. In this respect, the hypothesis is put forward that human beings must be endowed with some biologically determined, species-specific, universal computational mechanism (Lenneberg 1969). This mechanism, now called *Merge*, generates all possible hierarchical expressions of human language, by recursively assembling words into more complex syntactic objects (Chomsky 1995; Everaert et al. 2015; Friederici et al. 2017; Hauser, Chomsky, and Fitch 2002). *Merge* can be defined as a very simple combinatorial mechanism bringing two syntactic units together to recursively form new syntactic sets (7–8):

(7) $xy \rightarrow \{xy\}$
(8) $z\{xy\} \rightarrow \{z\{xy\}\}$

The syntactic category of the newly formed sets is assigned according to the labels of the items within the unit (9):

(9) $xy \rightarrow k_x\{xy\}$

Merge is taken to be intimately connected to the internal system of thought, independent of the sensory-motor system which externalizes thoughts via linear sequences of sounds, signs, or written characters (Chomsky 1995; Berwick et al. 2013).

Overall, early attempts within the generative framework to formalize the syntactic knowledge of language as the product of a biologically determined capacity present in all human beings has led to a deeper understanding of some of the key components of human language. More recent developments within the research program have promoted a significant shift toward a more biologically plausible

perspective on language (see Alexiadou and Lohndal, Chapter 3 this volume). Thus, these formalisms – although not exempt from critical opposing views (see the debate in *Natural Language and Linguistic Theory*: Holmberg 2000; Lappin, Levine, and Johnson 2000b, 2000a, 2001; Piattelli-Palmarini 2000; Reuland 2000; Roberts 2000; Uriagereka 2000) – have encouraged linguistics to seek integration with other sciences, including neuroscience, by putting forward possible testable models of language processing in the human mind (de Zubicaray and Schille 2019). The gradual emergence of noninvasive neuroimaging techniques investigating the structure and function of the human brain – electroencephalography (EEG), magnetoencephalography (MEG), functional/structural magnetic resonance imaging ([f]MRI) – has in turn opened to the possibility of validating such models, by looking for possible integration points between formal descriptions of human syntax and underlying neurobiological systems.

Moving from early lesion studies (Zurif, Caramazza, and Myerson 1972), the effort to test hypotheses about our abstract syntactic knowledge with neuroscientific methods has made it possible to begin evaluating the neurobiological validity of number of core aspects of human syntax – although a complete one-to-one correspondence between linguistic computations and neural processes might still be missing (Poeppel and Embick 2013). These include the testing of universal principles of grammar (Musso et al. 2003), the neural adherence to hierarchical constituency (Pallier, Devauchelle, and Dehaene 2011), the brain localization of recursive mechanisms for phrase-structure grammars (Friederici et al. 2006), and the neural response to basic structure-building computations under *Merge* (Zaccarella and Friederici 2015; Zaccarella et al. 2015). Current additional directions comprise the way the brain uses distinct cortical timescales to track compositional processing from words to sentences during language comprehension (Ding et al. 2016). At the phylogenetic level, the formalization of a possible computational syntactic system generating hierarchical linguistic structures has further enabled researchers to test the degree of species-specificity of language across human and nonhuman primates behaviorally (Hauser, Chomsky, and Fitch 2002), and with respect to their brains' function and structure (Milne et al. 2016; Milne, Petkov, and Wilson 2018; Wilson et al. 2015; Wilson et al. 2013) while at the same time enabling the comparison of the structural pathways subserving syntactic processing in the human brain with those found in the brains of nonhuman primates (Rilling et al. 2008).

The course of action in this chapter is as follows: We begin with a brief discussion of language as a biological system that includes a historical sketch of our understanding of language in the brain (Section 20.2). We continue with an overview of the early days of brain-syntax research in neuropsychology, primarily on the basis of lesion studies (Section 20.3). Next, we discuss some current insights on the neurobiological basis of syntactic computations in the adult brain derived from functional and structural imaging studies carried out in the past decades (Section 20.4 and Section 20.5). These results provide a more fine-grained picture of the core left-hemispheric networks involved in syntactic processing. An illustration of the structural correlates of syntactic abilities in ontogeny and phylogeny will follow (Sections 20.6 and 20.7). We end with a short summary of our discussion and a reflection on the impact that Noam Chomsky's ideas have had on the neuroscience of language.

20.2 Language as a Biological System

The link between language and the left hemisphere of the human brain was first established in 1836 by Marc Dax, a French neurologist who wrote a note about speech disturbance and left hemispherical lesions (published as Dax 1863; Dax 1865), 25 years before Paul Broca's more famous description of a patient whose lesion in the left inferior frontal cortex led to an arrest of speech (so-called aphemia; Broca 1861). Broca did not dissect the brains of his patients; therefore, he was not able to know that their lesions extended far into neighboring regions and the white matter (Dronkers et al. 2007). The posterior portion of the inferior frontal gyrus was soon termed Broca's area (Figure 20.1) and early language models considered it a speech-related brain region primarily supporting language production (Green 1970; Goodglass, Gleason, and Hyde 1970; Weigl and Bierwisch 1970). Further lesion studies associated the left superior temporal gyrus with language comprehension abilities (Wernicke 1874). Jointly, these observations gave rise to the Wernicke-Lichtheim-Geschwind (WLG) model of the neurobiology of language in which Broca's area subserves language production and so-called Wernicke's area (roughly left posterior superior temporal gyrus) enables language comprehension (Geschwind 1970; Lichtheim 1884). Although the WLG model correctly identified two major nodes in the language network, the model's anatomical assertions are nowadays severely underspecified, with incorrect functional attributions and impoverished linguistic description (Friederici 2011; Hagoort 2014; Tremblay and Dick 2016; but see Matchin and Hickok 2019, for an updated neural model that includes a neuroanatomical distinctions between language comprehension and production).
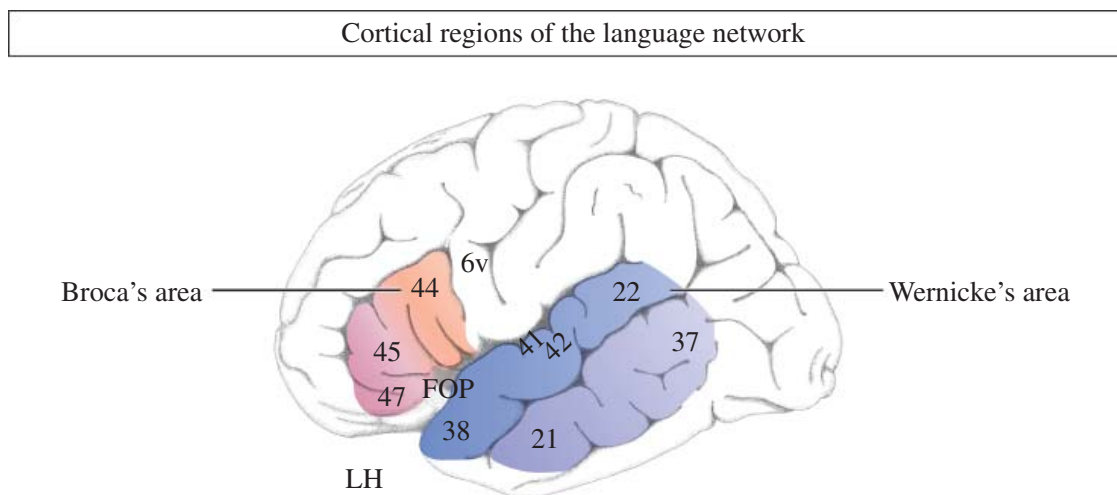
Figure 20.1 Cortical regions of the language network. Left hemispherical (LH) view of the human brain. Broca's area is located in the inferior frontal gyrus (IFG) and it is composed by Brodmann area (BA) 44 and BA 45. Additional classical regions in the IFG are the frontal operculum (FOP) and BA 47. Wernicke's region is located in the posterior temporal cortex (pTC). Cortical regions involved in language processing in the temporal cortex are the primary auditory cortex (BA 41/BA 42), the superior temporal gyrus (STG) (BA 22), the middle temporal gyrus (MTG) (BA 21) and BA 37, as well as the anterior temporal pole (BA 38)

20.3   The Early Days: Neuropsychological Evidence for Syntax in the Brain

Before the advent of functional neuroimaging, studying patients with brain lesions as well as patients undergoing neurosurgical interventions such as, for example, a corpus callosotomy (i.e. a split-brain operation) were the only way in which relationships between brain structure and cognitive functions could be established. Patients provided researchers with "natural experiments" that made it possible to draw inferences regarding the cognitive function supported by the destroyed tissue, given a patient's observed behavioral deficit or lack thereof due to a vascular disease (stroke), a brain contusion (accident) or after a surgical intervention. In line with the ideas of the WBL model mentioned above, traditional classifications of aphasic syndromes pay little attention to linguistic theory and instead tend to classify patients with regard to the loss of their language production or comprehension abilities. The loss or deficit of language production abilities is usually termed Broca's aphasia, whereas the loss or deficit of language comprehension abilities is labeled Wernicke's aphasia. We will here strictly focus on studies that are relevant to the neuroscience of syntax and abstain from discussing aphasiology and aphasic syndromes in any detail (see Raymer and Rothi 2015 for a general overview).

Zurif, Caramazza, and Myerson (1972) were the first to suggest that the aphasic syndrome leading to Broca's aphasia was not merely a language-production or speech-related deficit, as suggested by the WBL model in which Broca's area subserves language production and Wernicke's area supports language comprehension. Following linguistic theorizing of language competence to be distinct from performance, Zurif and colleagues reasoned that a competence deficit should affect performance both in production and comprehension. In their seminal work, the authors used a grammatical judgment task asking patients classified as Broca's aphasics – a subgroup of which usually exhibit behavior that is labeled as *agrammatic* in the literature – to sort words from a set of sentences on the basis of how closely related they thought the words would be. Zurif and colleagues found that the structures that the aphasic patients sorted excluded almost systematically all those grammatical elements (function words) that were not necessary part of the intrinsic meaning of the sentence, while retaining major lexical items. The authors thus concluded that "since the agrammatic aphasic's tacit knowledge of English syntax appears to be as restricted as is his use in syntax, we may presume that agrammatism reflects a disruption of the underlying language mechanism." Caramazza and Zurif (1976) tested Broca's aphasics' comprehension further, using center-embedded sentences that could be correctly understood either on the basis of semantic constraints ("the apple that the boy is eating is red"; semantically, only the boy can eat the apple, not vice versa), or on the basis of syntactic relationships among words ("the man that the woman is hugging is happy"; semantically, both the man and the woman can hug the other, while syntactically, only the woman can hug the man). Again, the authors found that Broca's aphasics performance dropped to chance when they had to use syntactic information. Thus, they proposed that these patients suffered from an impairment specifically related to "syntactic-like cognitive operations" in language comprehension *and* production caused by damage to the brain's "anterior language area" (i.e. Broca's area). A similar point of view was echoed by Friederici (1981) and Friederici, Schönle, and Garrett (1982) who asserted that the

deficit in agrammatic Broca's aphasics can be described as the inability of patients to assign syntactic structure.

The repeated association of agrammatic Broca's aphasia with frontal lesions led Grodzinsky (2000) to eventually put forward the so-called trace-deletion hypothesis. This hypothesis constituted a first attempt at establishing explicit links between an aphasic syndrome (Broca's aphasia), a brain region (Broca's area), and a specific linguistic theory (Government-and-Binding [GB] theory; Chomsky 1988). More precisely, the central claim of the trace-deletion hypothesis was that Broca's area implements cognitive functions that relate to the movement of phrasal constituents, but only with regard to noun phrases and *wh*-phrases, excluding head-movement. Grodzinsky thus considered the impairment of Broca's aphasics to be related to one very particular aspect of linguistic theory, whereas the general ability to build phrases or for syntactic processing construed more broadly was thought be preserved in these patients.

While recent developments within the Minimalist framework challenge the trace-deletion hypothesis at the theoretical level (Nunes 2011), the very coarse neuroanatomical precision of the lesion areas due to vascular diseases is a general downside of aphasia studies. Moreover, the notion of Broca's area has been defined in many different ways by different researchers (Tremblay and Dick 2016). Today, Broca's area is understood to be neither cytoarchitectonically nor functionally homogenous (Amunts and Zilles 2012; Goucha and Friederici 2015; Hagoort 2013; Hagoort and Indefrey 2014; Zaccarella, Schell, and Friederici 2017; Zilles and Amunts 2018). Against this background, the general observation that lesions are rarely focal and tend to encompass more than just one particular brain region becomes crucial. More recent work in aphasiology has tried to overcome some of these limitations using a so-called lesion-symptom mapping approach relying on the overlap of many individual lesions (for a review see Wilson 2017) but the general reservations still hold.

In sum, lesion studies have been a reliable tool for establishing first brain–behavior relationships, showing that syntactic abilities are lateralized and, to an extent, depend on the posterior portion of the inferior frontal gyrus in the language dominant hemisphere. But mapping linguistic computations onto neural circuitry requires an approach that captures the computational machinery of the human language faculty in more parsimonious and generic (i.e. Minimalist) terms and, at the same time, provides a much more fine-grained assessment of the involved neural structures on the neuroscientific side. The advent of structural and functional neuroimaging has provided researchers with a tool capable of obtaining such fine-grained data which we can attempt to link to linguistic computations.

20.4   Functional Imaging of Syntactic Computations

A great number of studies across different experimental manipulations in different languages and modalities have been testing the neuroanatomical reality of the syntactic component, by specifically looking at:

- Universal principles of grammar by means of possible and impossible syntactic rules
- The brain's adherence to hierarchical constituency
- Movement

- Degree of recursion
- The *Merge* computation

Overall, syntactic processing appears to be strongly localizable in the left hemisphere, including Broca's area, and specifically in BA 44, the posterior superior temporal gyrus (pSTG) and the superior temporal sulcus (pSTS; Friederici 2011; Hagoort and Indefrey 2014; Zaccarella, Schell, and Friederici 2017). Here, we discuss some representative functional studies testing syntax in the brain. This list of studies is by no means intended to be exhaustive, but it tries to broadly cover some of the most central issues on natural language syntax tested using functional imaging in the mature brain.

In a seminal study comparing possible and impossible grammars, Musso and colleagues had German native speakers learn sets of grammatical rules of the Italian and the Japanese languages that could either be real or unreal in the sense that they would violate general syntactic principles of human grammar (Musso et al. 2003). Subjects would either learn a language that, for example, used lexical elements from real Italian and required a linguistic parameter setting different from the subjects' native German (e.g., the null-subject parameter: *Mangio la pera.*, literally "eat the pear" with the meaning "I eat the pear"), or a language that used lexical elements from real Italian but relied on an impossible rule (e.g., negation being established by arbitrarily emphasizing a specific linear position of a word in the sequence instead of using hierarchy: *Paolo mangia la no pera.*, literally "Paolo eats the no pear"). The authors report a change of activation in Broca's area throughout the course of the functional neuroimaging study, with an increase of activation in later runs (when, presumably, subjects have mastered novel rules) relative to earlier runs (when, presumably, subjects are still learning the rules). Critically, this increase only occurred for languages with rules that agreed with structure-dependent rules of Universal Grammar as posited in generative grammar, and not for languages with rules that depended on linear order and not structure. The same patterns of data in Broca's area had also been reported when different stimuli and population samples were tested, still manipulating real and impossible syntactic rules (Tettamanti et al. 2002).

The neural adherence to hierarchical constituency has first been tested by Pallier and colleagues using fMRI to measure neural activity correlating with constituent size of linguistic structures (Pallier, Devauchelle, and Dehaene 2011). Specifically, subjects were asked to read sequences of 12 words or pseudowords, which could form constituents of 12-word length ("I believe that you should accept the proposal of your new associate"), or being decomposed in smaller constituents of reduced size, like 6 ("the mouse that eats our cheese; two clients examine this nice couch"), 4, 3, or 2 while lying in the scanner. The authors found a set of areas in the left posterior temporal and inferior frontal regions, including Broca's area, showing constituent size effects regardless of whether the constituents were formed by real content words, or whether they were replaced by pseudowords. This suggests that these areas are able to access abstract syntactic frames to build well-formed constituent structures, even in the absence of semantic meaning. On the other hand, regions in the temporal pole, anterior superior temporal sulcus and temporo-parietal junction showed constituent size effect only in the presence of real content words.

The linguistic concept of *movement* describes word order permutations by having discontinuous constituents or displacements within a sentence (see Nunes 2011 for a re-definition of movement in Minimalist terms). A study by Ben-Shachar et al. (2003)

in Hebrew and found that movement could be localized in the left inferior frontal gyrus (i.e. Broca's area) and in the pSTS and suggested that the structural analysis of sentences containing syntactic movement may take place in Broca's area, while access to predicate argument structure might occur in the left pSTS. Friederici et al. (2005) showed that the activation in the posterior portion of Broca's area (BA 44) parametrically increased as the number of moved constituents increased. In this study, activation was also found in the presupplementary motor area though this activation did not change with the number of moved constituents.

Functional studies on recursion have been motivated by the attempt to test how the human brain might handle grammars of increasing generative power, ranging from low-level AB^n finite-state grammars (FSG) based on transitional probabilities, to more complex A^nB^n phrase-structure grammars (PSG) that can generate structures of natural human languages. In one first artificial grammar fMRI experiment, Friederici and colleagues could show that the two grammars are supported by different areas in the human brain, such that the FSG processing is subserved by the left frontal operculum, while the posterior portion of Broca's area (BA 44), a phylogenetically younger cortical area, appears to be specifically active during the computation of PSG dependencies (Friederici et al. 2006). In a second experiment using a natural grammar and German sentences as stimuli, PSG rules generating double-embedding structures ("Maria, [die Hans, [der gut aussah], liebte], Johan geküsst hatte]"*; Maria who loved Hans who was good looking kissed Johan*) also revealed activation in BA 44 driven by syntactic complexity operationalized as the number of embedded sentences (Makuuchi et al. 2009). The latter study in contrast to the former study, using natural meaningful sentences, additionally activated the posterior superior temporal cortex (Friederici et al. 2009).

In recent years, different imaging studies have begun to reduce stimulus complexity to very basic two or three-word levels to determine the localization of single applications of *Merge* in the human brain (Schell, Zaccarella, and Friederici 2017; Zaccarella and Friederici 2015; Zaccarella et al. 2015). By using determiner phrases with very reduced conceptual content consisting of a function word and a pseudoword ("Dieser Flirk"; *This flirk*), it was possible to localize *Merge* in a very confined subpart of the most anterior-ventral BA 44 with little variance across subjects. List strings without any function word, in contrast, only involved the frontal operculum/anterior insula (Zaccarella and Friederici 2015) – a phylogenetically older part of the cortex (Sanides 1962; Amunts and Zilles 2012). Thus, these results converge on the idea that specific neural populations of BA 44 are especially active during *Merge* application, be it at very basic levels or more complex ones, also in the absence of semantic information (Goucha and Friederici 2015).

To note, converging evidence for the existence of a neural syntactic component building-up hierarchical linguistic structures can be finally found in recent neurocognitive approaches using online parsing information metrices that aim to test neural behavior correlating with linguistic competence during actual performance (Brennan 2016). First studies report that hierarchy-based parsing models (Brennan et al. 2016; Nelson et al. 2017; Bhattasali et al. 2019; Brennan and Hale 2019; see also Ding et al. 2016 and Martin and Doumas 2017) outperform linear-based models (for a discussion on linear-based models, see Frank and Yang 2018; Frank and Christiansen 2018; Frank, Bod, and Christiansen 2012; McDonald and Shillcock 2003) in explaining

unique variance in neural activation within the cortical language network during natural language processing, notwithstanding distinct temporal resolutions and different methodologies employed.[1]

20.5   Functional and Structural Connections of the Syntactic Network

At the functional level, methods of analysis estimating the directionality of information flow between specific regions during experimental stimulation (Dynamic Causal Modeling, DCM; Friston, Harrison, and Penny 2003) has made it possible to observe how regions active for syntactic tasks might co-work during phrase structure building. One first study found that syntactic complexity – operationalized as complex object-cleft vs. less complex subject-cleft sentences – appears to be primarily processed in the IFG – which acts as a pure syntactic processor – and then sent to the pSTS/STG, which seems to rather support verb argument structure (den Ouden et al. 2012). The centrality of the IFG as the driving input for syntax has been confirmed by further studies using either complex object-first sentences (Makuuchi and Friederici 2013) , or very simple two-word phrases (Wu, Zaccarella, and Friederici 2019), thus suggesting
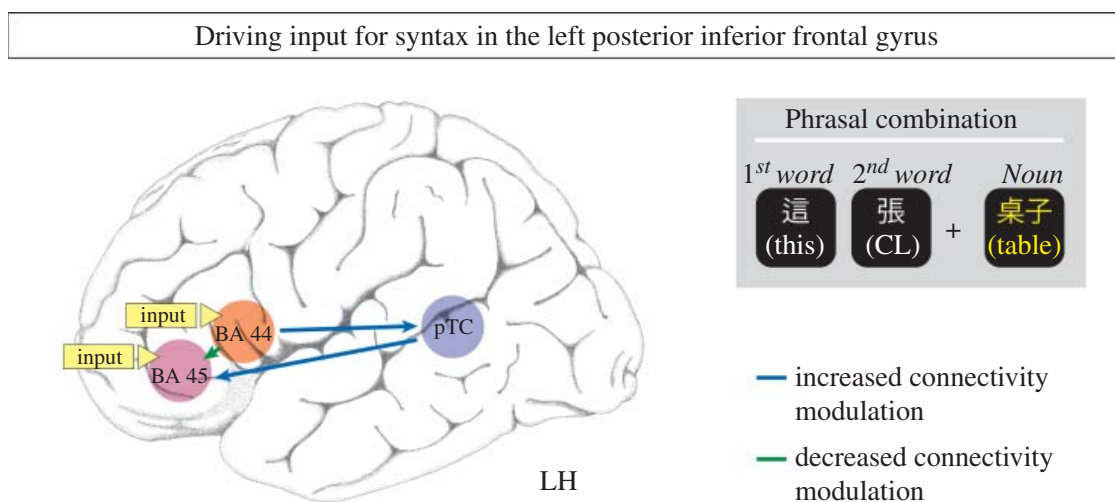
Figure 20.2   Driving input for syntax in the left posterior inferior frontal gyrus. Functional modulations of the linguistic network during the processing of simple phrases in Chinese. The driving input in left BA 44 and 45 indicates that the IFG takes over syntactic and semantic information processing at the initial state of word recognition in Chinese. The connection from BA 44 to BA 45 is strongly inhibited during the processing of syntactically grammatical sequences, suggesting that BA 44 inhibits semantic information processing in BA 45 to resolve the phrase structures (green arrow). The strong modulations in the connections from BA 44 to the posterior temporal cortex (pTC) and from pTC to BA 45 reflect lexico-semantic integration processing. *Source*: Adapted from Wu, Zaccarella and Friederici, (2019)

IFG's primary role in phrase structure building independently of hierarchical complexity (Figure 20.2). Worth noting is the observation that activity in BA 44 and in the pSTS/STG during language experiments have been found to correlate with each other already when modulatory effects driven by linguistic manipulations are removed from the signal, indicating the existence of a basic network acting as a general framework for language processing (Lohmann et al. 2010).

At the structural level, diffusion tensor imaging (DTI) has made it possible to identify structural connections between brain regions in vivo (Catani and Thiebaut de Schotten 2008), thus revealing distinct dorsal and ventral white matter fiber bundles connecting the inferior-frontal with posterior temporal regions (Figure 20.3). The dorsal pathway linking the posterior Broca's area (BA 44) with the posterior temporal cortex via the arcuate fascicle has been demonstrated to correlate with the ability to perform syntactic processes (Friederici et al. 2006; Skeide and Friederici 2016; Wilson et al. 2011). Further evidence in this respect comes from structural data based on probabilistic tractography, which show that the activation peak in BA 44 obtained from the PSG artificial grammar paradigm based on nonadjacent hierarchical dependences (A^nB^n) connects with the pSTG along the dorsal pathway. Results from DTI-based tractography propose that the ventral pathway linking BA 47 and anterior Broca's area (BA 45) to the temporal cortex via the extreme fiber capsule system rather supports semantic processing (Saur et al. 2008).

Overall, the precise neuroanatomical characterization of the linguistic network implementing syntax makes it possible to ask whether this network is already present at birth and how it develops during maturation (ontogeny), as well as whether this network is present in the brains of nonhuman primates and how it evolved (phylogeny). These neuroscientific questions are directly related to Chomsky's insight that crucial aspects of the syntactic component are innate and that it is unique to our species. These issues will be discussed in turn in the two following sections.
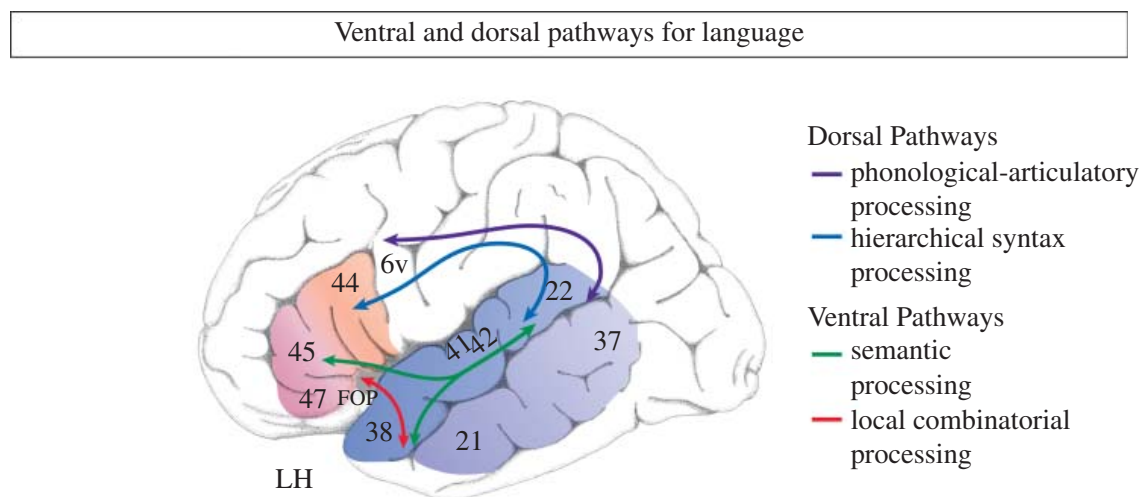
Figure 20.3   Ventral and dorsal pathways for language. Left hemispherical (LH) view of the human brain showing the two main dorsal pathways involved in syntactic processing and articulation and two main ventral pathways involved in local combinations and semantic processing in general. This model is based on data from both functional and anatomical neuroimaging. *Source*: Adapted from Goucha, Zaccarella, and Friederici (2017)
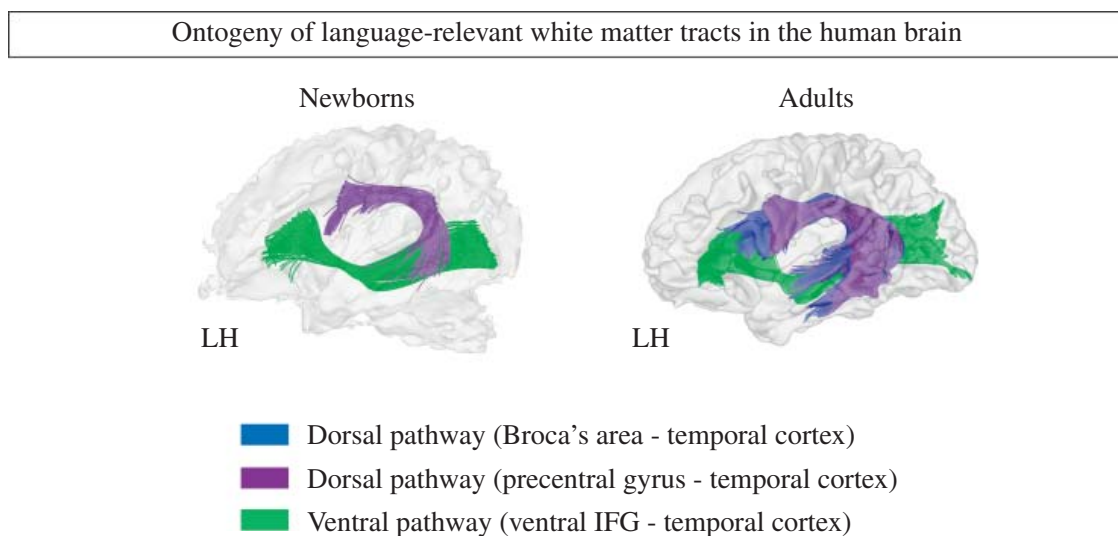
20.6   Ontogeny

Empirical questions concerning the maturation of the linguistic network implementing syntax abilities in children include the degree of functional specialization of the language-relevant regions for syntactic processes, the shift between intrahemispheric to interhemispheric functional connections of the linguistic network, and the maturation of the ventral and dorsal tracts linking frontal and posterior temporal regions anatomically.

The ability to handle grammatical complexity in children is not fully mastered at least until the first seven years of life (Skeide and Friederici 2016). A first functional study testing syntactic complexity and semantics with plausible and implausible subject- and object-relative clauses in three age groups (3-4 years old; 6-7 years old, 9-10 years old) found that the adult dissociation between syntax and semantics on the neural level cannot be observed in children until the age of 7, as shown by syntax-semantics interactions in the left pSTG/mSTG, with involvement of the inferior-frontal regions below statistical threshold (Skeide, Brauer, and Friederici 2014). Only around the end of the tenth year of life children begin to approach first syntax-specific responses in the left IFG. BA 44 however does not seem to be fully specialized for complex syntax as in older children and adults yet (Nuñez et al. 2011), but it rather works coactively with more anterior regions in BA 45. Notably, another functional study could further show that increased neural activity in the left temporal regions – and to a lesser extent in BA 44 – can already be appreciated in five-year-old children with better syntactic proficiency in using case-marking cues during object- vs. subject-first sentences processing (Wu et al. 2016). A similar strong association between accuracy performance and functional activation in the temporo-frontal network was confirmed by a large correlational study across four age groups ranging from three years of age to young adulthood (Skeide, Brauer, and Friederici 2015). Collectively, these findings suggest that the neural resources for the development of syntactic knowledge initially primarily recruit the posterior superior temporal cortex, and only later they shift toward BA 44 as a function of age and proficiency.

When looking at changes in functional connectivity between pSTG and Broca's area, the coordination between these two regions as observed in the mature brain during speech and language processing only develops gradually from early infancy to adulthood (Dehaene-Lambertz, Dehaene, and Hertz-Pannier 2002; Perani et al. 2011). Whereas the adult brain exhibits a marked lateralization and intrahemispheric functional connectivity between Broca's area and pSTG, newborns show interhemispheric connectivity between these regions in the left hemisphere and their respective right-hemipsheric homologues, mainly between the superior temporal regions (Friederici, Brauer, and Lohmann 2011). The mature pattern of lateralization and increased functional connectivity between Broca's area and left pSTG can only be observed at around six years of age when using task-free measures such as resting-state fMRI (Xiao et al. 2016), thus indicating that maturation of the core language network ultimately leads to an increased specialization and functional segregation of the processing of semantic and syntactic information (Skeide, Brauer, and Friederici 2014).

Investigations into the anatomical development of brain functions, including language, move from the fact that while brain function relies on the transmission of electrical impulses from one brain region to another via white-matter pathways, the efficiency of information transmission is determined by the degree of myelination

of a particular fiber tract (Nave and Werner 2014; Wake, Lee, and Fields 2011). Different fiber tracts in the human brain exhibit distinct developmental trajectories as evidenced by their different degrees of myelination during maturation (Dubois et al. 2008; Lebel et al. 2012; 2008; Pujol et al. 2006). Crucially, the dorsal fiber tract connecting pSTG to BA 44 develops rather late during childhood and its degree of myelination is highly predictive for a child's capacity to process hierarchically complex sentences (Brauer, Anwander, and Friederici 2011; Skeide, Brauer, and Friederici 2016; Skeide and Friederici 2016). Conversely, the dorsal pathway targeting premotor cortex and the ventral pathway targeting BA 45 and more anterior portions of the inferior frontal gyrus area already well myelinated early on in life and thus highly functioning (Figure 20.4). These pathways support phonological learning during early infancy (Friederici, Mueller, and Oberecker 2011; Kuhl et al. 2006). As a matter of fact, analyses of the cortical microstructure measuring the volume of cell bodies in Broca's area indicate that leftward asymmetry in BA 44 is only visible around the age of 11 years, whereas leftward asymmetry of BA 45 is already present much earlier around 5 years of age (Amunts et al. 2003). Taken together, the maturation of the structural network including BA 44 in the IFG and the dorsal connection to the posterior temporal cortex appear to be crucial to the mastering of syntax processing in natural language.

Ontogeny of language-relevant white matter tracts in the human brain

Newborns Adults

LH LH

■ Dorsal pathway (Broca's area - temporal cortex)
■ Dorsal pathway (precentral gyrus - temporal cortex)
■ Ventral pathway (ventral IFG - temporal cortex)

adapted from Perani et al., 2011

Figure 20.4 Ontogeny of language-relevant white matter tracts in the human brain. Left hemispherical (LH) view of the newborn brain (left) and the adult brain (right) showing fiber tracking of diffusion tensor imaging data seeding in Broca's area and in the precentral gyrus/premotor cortex. Ventrally, the pathway connecting the ventral inferior frontal gyrus to the temporal cortex is present in both adults and newborns (extreme capsule, green). Dorsally, the adults show two pathways – one connecting the temporal cortex to Broca's area (arcuate fasciculus and superior longitudinal fasciculus, blue), and one connecting the temporal cortex to the premotor cortex (purple). In newborns, only the pathway to the premotor cortex can be detected whereas the connection to Broca's area matures late. *Source*: Adapted from Perani et al. (2011)

The initially weak structural integrity of the core language network raises the question as to how this relatively late maturation for complex syntax might nonetheless enable young children to begin mastering more basic merging combinations. Behavioral studies put forward the hypothesis that very young children might already be able to produce determiner-noun combinations ("the cat" or "a cat"), by freely combining determiners and nouns according to syntactic rules (Yang 2013), even in case of sensory-deprivation due to deafness and lack of systematized linguistic input (Goldin-Meadow and Yang 2017). Neural evidence further supports the idea that very young children might be already able to detect local phrase structure violations in the linguistic stream (Bernal et al. 2010; Brusini et al. 2016). During early childhood, linguistic processing might possibly depend on the pathways targeting the ventral connections to the IFG in order to allow for basic structure building (i.e. a single application of *Merge*). In contrast, the delayed processing of more complex recursive structures additionally require working memory resources in the more dorsal portions of Broca's area (Makuuchi et al. 2009), extending along the dorsal pathway to the posterior temporal cortex via the inferior parietal regions (Fengler, Meyer, and Friederici 2016; Meyer et al. 2012; Grossman et al. 2002). Following Chomsky's more recent ideas about language acquisition – i.e. the vast majority of the acquisition process may be dedicated to acquiring lexico-semantic knowledge specific to (externalization of) the target-language (Berwick and Chomsky 2016) – the working hypothesis is put forward that neural activity related to syntactic processing in the inferior frontal regions might be initially overshadowed by lexico-semantic processing in posterior temporal cortex, notwithstanding behavioral reliance on syntactic knowledge early on in life.

20.7   Phylogeny

From an evolutionary point of view, the neural mechanisms for syntactic structure building could have evolved in nonhuman species either via evolutionary convergence with an only distantly related species (e.g., songbirds), or by descent from a common primate ancestor (Bolhuis et al. 2014). Despite these principled reasons and continuous efforts to discover homologies of human language in nonhuman primates, there is so far no empirical evidence that any nonhuman species has evolved a system with the computational capacity exhibited by the human syntactic system (Beckers et al. 2012; Berwick et al. 2013; 2011; Bolhuis, Okanoya, and Scharff 2010; Bolhuis et al. 2014; Yang 2013). Given that the comparative method has been the standard approach to the study of language evolution a potentially demoralizing conclusion follows, namely that if language is specific to the human species then there actually may be "not much to compare" (Bolhuis et al. 2014).

The fact that we now have a solid neuroanatomical characterization of the core language network that subserves syntactic processing in humans invites cross-species comparisons to go beyond behavioral studies which have compared the performance of humans and nonhuman primates on comprehension and production tasks involving symbol combination and sequence processing (for a review see Friederici, in press). So far, all studies comparing the performance of humans and nonhuman primates on comprehension and production tasks involving symbol combination and sequence processing converge on the fact that nonhuman primates lack systematic combinatorics as they do not approach the ability of processing hierarchical sequences

that go beyond linear combinations (Fitch and Hauser 2004; Hauser, Chomsky, and Fitch 2002).

This conclusion holds up independent of the modality of language use and can therefore not be attributed mechanisms for vocal learning, as the use of sign language stimuli in studies with nonhuman primates has yielded similar results (Terrace et al. 1979; Yang 2013). Along these lines, a recent study analyzing the brain's white matter structure in hearing subjects and early deaf signers revealed a separation of the neural network for language and speech (Finkl et al. 2019). While no group difference was found for the language network, significant differences were found for the speech-related network, thereby providing further neural evidence for a separation between language and speech as postulated by Chomsky (Chomsky 1995, 2005; Friederici et al. 2017).

Converging on these conclusions, comparative functional neuroimaging studies have shown that the learning of linear sequences in nonhuman primates and humans differentially recruited frontal cortex in an interesting pattern: while macaques showed activation in the homologue to Broca's area – the ventral frontal opercular cortex – in response to simple forward-branching violations, neural activation in response to violations in humans was found in the frontal operculum in the ventral frontal cortex but not in Broca's area (Wilson et al. 2015). As monkeys appear to be able to learn non-hierarchical rule-based sequences, this has been suggested to be a possible phylogenetic precursor of phrase-structure processing in humans, and a possible cross-correspondence with language development in children (Friederici 2017).

The functional differences in the recruitment of frontal cortex during sequence processing and the apparent inability of nonhuman primates to process hierarchically structured phrases are also evidenced in differences with regard to brain structure and connectivity across species which parallel the immaturity of this network in humans in infancy. Cortical terminations of the arcuate fasciculus as the fiber pathway connecting Broca's area and pSTG in humans differ considerably between humans and nonhuman primates (Rilling et al. 2008; Perani et al. 2011). Moreover, cytoarchitectonic analyses reveal that, compared to humans, nonhuman primates like chimpanzees exhibits no leftward asymmetry, either in BA 45 or in BA 44 (Schenker et al. 2010). This regional asymmetry in humans compared to nonhuman primates is accompanied by a strong asymmetry of the arcuate fasciculus itself (Rilling et al. 2012; Rilling et al. 2008; Rilling 2014), thus pointing toward the view that dorsal fiber tract connecting BA 44 to the pSTG/STS might constitute a crucial neural precondition for linguistic humaniqueness – the capacity of handling hierarchical linguistic structures – to take place along evolution (Goucha, Zaccarella, and Friederici 2017).

20.8   Conclusion

In this chapter we discussed neuroanatomical evidence supporting humans' capacity to handle linguistic hierarchies. We started out from the view that human language results from a biologically determined grammar system generating linguistic sequences out of abstract hierarchical relations between words (Chomsky 1965, 1981, 1995). We first gave an overview of the early days of brain-syntax research and focused on those lesion studies assessing the cognitive nature of specific language impairments like agrammatism in Broca's aphasics. We stressed the importance of seminal works

using grammatical judgments to test language competence beyond prior performance distinctions between production and comprehension (Zurif, Caramazza, and Myerson 1972). Such studies paved the way to the emergence of modern neurobiology of language as the discipline linking together language and the brain, by using experimental methodologies to test theoretical predictions from linguistic theory at the neural level. In the central part of the chapter we discussed current objectives on the neuroanatomical reality of the syntactic component, isolating a fronto-temporal network in the left hemisphere that comprises the connection between BA 44 and posterior temporal cortex along the dorsal fiber track. We provided compelling neural evidence for a number of core aspects of human syntax put forward within the generative framework, including the existence of universal principles of grammar, neurally represented, which distinguish possible and impossible syntactic rules (Musso et al. 2003); the functional reality of hierarchical constituency (Pallier, Devauchelle, and Dehaene 2011); movement (Friederici et al. 2005); mechanisms of recursion (Friederici et al. 2006); the implementation of *Merge* (Zaccarella and Friederici 2015); and the time course dynamics driving the internal construction of hierarchical linguistic structure (Ding et al. 2016; Nelson et al. 2017). We then sketch out the development of the functional and structural network during childhood, giving an overview of maturation stages of the dorsal pathway for the mastering of syntax processing in natural language (Skeide and Friederici 2016). We concluded with the hypothesis that the dorsal fiber tract connecting BA 44 to the pSTG/STS might constitute a crucial neurological precondition for our capacity of handling hierarchical linguistic structures to emerge (Goucha, Zaccarella, and Friederici 2017).

We would like to end this chapter with a reflection on the legacy that Chomsky's ideas have had on the neuroscience of language. Such a legacy is according to us essentially twofold: the view of language as a biological system which is implemented in the human brain, and the idea that grammar and performance factors do not equate each other. These two aspects, we believe, are necessarily subsumed in any study approaching language in experimental settings. Such studies have in this sense offered empirical validation for the biological reality of core claims about the human capacity for language, as put forward in generative grammar and within the Minimalist framework. More importantly, they call for an increased collaboration between linguists and neuroscientists to bring the relation between linguistic phenomena and neural data to a deeper level of understanding (Friederici and Singer 2015; Poeppel 2012).

Conflicts of Interest

None of the authors has conflicts of interest to declare.

Acknowledgments

Endnote

1   Overall, these studies attempt to implement plausible neuro-computational models involving an incremental parser that can track the on-line unfolding of linguistic strings, together with some linking hypothesis connecting parser states to neural signals (Brennan 2016). The specific parsing states depend on the relative strategy that a parser adopts – expansion (top-down), reduction (bottom-up), projection (left-corner) – according to a certain constituency grammar – e.g., context-free grammar, Minimalist grammar (Hale et al. 2015; Hale 2014; Li and Hale, 2019). The linking hypothesis would then correspond to some complexity metrics indexing each specific state of the parser – e.g., the node count for a specific word based on the different parsing strategy. In this respect, hierarchy-based models attempt to observe neural behavior correlating with phrase structure during actual performance, on the basis of detailed on-line parsing algorithms by which linguistic knowledge might be explicitly implemented (Bhattasali et al. 2019; Nelson et al. 2017). While such approaches remain necessarily agnostic with respect to structure-building operations per se, as they only test general parsing assumptions, improved performance-oriented approaches using more transparent translational hypothesis to test structure-building operations are now emerging (Chesi 2012; 2014; Chesi and Canal 2019; Fong 2014).

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