1   Neuroscience and syntax

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37 **Abstract**

38 The neuroscience of language uses experimental methodologies from cognitive science and

39 neuroscience to investigate the neurobiological basis of linguistic phenomena in the human

40 brain. In this chapter, we review neuroanatomical evidence for the human capacity to handle

41 linguistic hierarchies, in line with the Chomskyan view of language as a biologically

42 determined system computing abstract relations between words to generate grammatical

43 linguistic sequences. We first focus on seminal neurological lesion studies assessing specific

44 language impairments like agrammatism in patients with Broca's aphasia. We stress the impact

45 that this work has had on the development of neurolinguistics by highlighting the need to go

46 beyond distinctions between language production and comprehension to investigate language

47 competence at the basis of grammatical knowledge. In the central part of the chapter, we review

48 current neuroscientific perspectives on the core aspects of human language put forward within

49 the generative framework: universal principles of grammar, constituency, recursion, and

50 Merge. We will provide evidence in favor of a fronto-temporal network in the left hemisphere

51 comprising the connection between Brodmann area (BA) 44, the posterior portion of Broca's

52 area, and the posterior temporal cortex along a dorsal fiber track crucial for syntactic

53 processing. The temporal dynamics driving the internal construction of hierarchical linguistic

54 structure will be also introduced. An overview of maturational stages of the dorsal pathway

55 and their relevance for the mastering of syntax will then be sketched out. We conclude by

56 putting forward the hypothesis that the dorsal fiber tract connecting BA 44 to the posterior

57 temporal cortex may constitute a crucial neurological precondition for the emergence of the

58 human capacity of handling hierarchical linguistic structures. On this account, we believe that

59 Chomsky's notion of language as a biological system and the study of grammatical competence

60 as distinct from performance factors have had and will continue to have profound implications

61   for neuroscientific approaches to the study of language. Therefore, increasing collaboration

62   between linguistics and neuroscience is strongly desirable to bring the relation between neural

63   data and linguistic phenomena to a deeper level of understanding.

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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 the present 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.
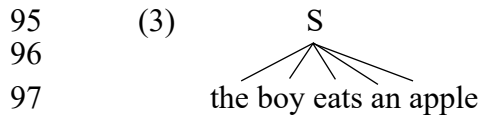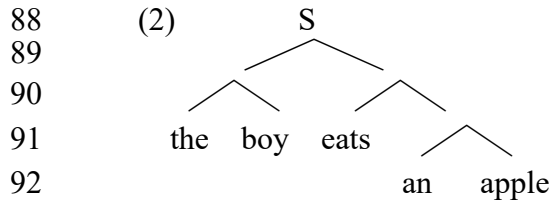
A detailed characterization of the fundamentally hierarchical nature of human language has been already at the heart of linguistic theory since the advent of the generative enterprise in the second half of the previous century. A major objective within the generative framework has been to make humans' 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

88　(2)　　　　　S

90

91　　　the　boy　eats

92　　　　　　　　　　an　　apple

93
94
95　(3)　　　　　S

96
97　　　　the boy eats an apple

98

99　Empirical tests on tree structures　like (2) and (3) exist, which can be used to assess the

100　superiority of hierarchy over linearization, by showing that some sequences of words behave

101　as units when certain syntactic manipulations are applied to the sentence (see "constituent

102　analysis"; Harris, 1946; Nida, 1948; Pike, 1943; Wells, 1947). For example, a syntactic unit

103　like *an apple* in (4) can be focus in a cleft construction in (5), while non-units, like *apple in*

104　cannot in (6):

105　　　(4) The boy eats an apple in the park

106　　　(5) It is an apple that the boy eats __ in the park

107　　　(6) *It is apple in that the boy eats an __ the park

108　The absence of any intermediate phrasal level between single words and the sentence node in

109　(3) above would not be able to predict the possibility of dislocating units within the sentence,

110　nor any asymmetry between (5) and (6). The discovery that certain relations (e.g. c-command;

111　Reinhart, 1976) regulate binding between distinct units in the sentence (e.g. anaphors and

112　antecedents) according to pervasive structure-dependent principles has considerably

113　strengthened the hierarchically-based hypothesis for language expressions.

114   Developments within the generative framework in the last decades have concentrated on the

115   precise characterization of the mechanism enabling hierarchical structures to be generated. In

116   this respect, the hypothesis is put forward that human beings must be endowed with some

117   biologically determined, species-specific, universal computational mechanism (Lenneberg

118   1969). This mechanism, now called *Merge*, generates all possible hierarchical expressions of

119   human language, by recursively assembling words into more complex syntactic objects

120   (Chomsky, 1995; Everaert, Huybregts, Chomsky, Berwick, & Bolhuis, 2015; Friederici,

121   Chomsky, Berwick, Moro, & Bolhuis, 2017; Hauser, Chomsky, & Fitch, 2002). *Merge* can be

122   defined as a very simple combinatorial mechanism bringing two syntactic units together to

123   recursively form new syntactic sets (7-8):

124   (7) *xy* ➔ *[xy]*

125   (8) *z[xy]* ➔ *[z[xy]]*

126   The syntactic category of the newly formed sets is assigned according to the labels of the items

127   within the unit (9):

128   (9) *xy* ➔ k_x*[xy]*

129   *Merge* is taken to be intimately connected to the internal system of thought, independent of the

130   sensory-motor system which externalizes thoughts via linear sequences of sounds, signs, or

131   writing characters (Chomsky 1995; Berwick et al. 2013).

132   Overall, early attempts within the generative framework (see Barksy, this volume for a

133   historical perspective) to formalize the syntactic knowledge of language as the product of a

134   biologically determined capacity present in all human beings has led to a deeper understanding

135   of some of the key components of human language. More recent developments within the

136 research programm have promoted a significant shift towards a more biologically plausible

137 perspective on language (see Alexiadou & Lohndal, this volume). Thus, these formalisms—

138 although not exempt from critical opposing views (see the debate on NLLT: Holmberg, 2000;

139 Lappin, Levine, & Johnson, 2000b, 2000a, 2001; Piattelli-Palmarini, 2000; Reuland, 2000;

140 Roberts, 2000; Uriagereka, 2000)—have encouraged linguistics to seek integration with other

141 sciences, including neuroscience, by putting forward possible testable models of language

142 processing in the human mind (de Zubicaray and Schille 2019). The gradual emergence of non-

143 invasive neuroimaging techniques investigating the structure and function of the human

144 brain—electroencephalography (EEG), magnetoencephalography (MEG),

145 functional/structural magnetic resonance imaging ([f]MRI)—has in turn opened to the

146 possibility of validating such models, to look for possible integration points between formal

147 descriptions of human syntax and underlying neurobiological systems.

148 Moving from early lesion studies (Zurif, Caramazza, and Myerson 1972), the effort to test

149 hypotheses about our abstract syntactic knowledge with neuroscientific methods, has made it

150 possible to begin evaluating the neurobiological validity of number of core aspects of human

151 syntax—although a complete one-to-one correspondence between linguistic computations and

152 neural processes might still be missing (Poeppel & Embick, 2013). These include the testing

153 of universal principles of grammar (UG; Musso et al., 2003), the neural adherence to

154 hierarchical constituency (Pallier, Devauchelle, & Dehaene, 2011), the implementation of

155 recursive mechanisms for phrase-structure grammars (Friederici, Bahlmann, Heim, Schubotz,

156 & Anwander, 2006), and the neural response to basic structure-building computations under

157 *Merge* (Zaccarella & Friederici, 2015; Zaccarella, Meyer, Makuuchi, & Friederici, 2015).

158 Current additional directions comprise the way the brain uses distinct cortical timescales to

159 track compositional processing from words to sentences during language comprehension

160   (Ding, Melloni, Zhang, Tian, & Poeppel, 2016). At the phylogenetic level, the formalization

161   of a possible computational syntactic system generating hierarchical linguistic structures has

162   further enabled researchers to test the degree of species-specificity of language across human

163   and non-human primates behaviorally (Hauser, Chomsky, & Fitch, 2002), and with respect to

164   the brains' function and structure (Milne et al., 2016; Milne, Petkov, & Wilson, 2018; Wilson

165   et al., 2015; Wilson et al., 2013) while at the same time enabling the comparison of the brains'

166   structural pathways subserving syntactic processing in the human brain with those found in the

167   brain of non-human primates (J. K. Rilling et al. 2008).

168   The course of action in this chapter is as follows: We begin with a brief discussion of language

169   as a biological system that includes a historical sketch of our understanding of language in the

170   brain (§. 2). We continue with an overview of the early days of brain-syntax research in

171   neuropsychology, primarily on the basis of lesion studies (§. 3). Next, we discuss some current

172   insights on the neurobiological basis of syntactic computations in the adult brain derived from

173   functional and structural imaging studies carried out in the past decades (§. 4-5). These results

174   provide a more fine-grained picture of the core left-hemispheric networks involved in syntactic

175   processing. An illustration of the structural correlates of syntactic abilities in ontogeny and

176   phylogeny will follow (§. 6-7). We end with a short summary of our discussion and a reflection

177   on the impact that Noam Chomsky's ideas have had on the neuroscience of language (§. 8).

178   **2. Language as a biological system**

179   The link between language and the human brain was first established in 1836 by Marc Dax a

180   French neurologist who published a respective note (published as Dax, 1863; Dax, 1865),

181   twenty-five years before Paul Broca's more famous description of a patient whose lesion in the

182   left inferior frontal cortex led to an arrest of speech (so-called aphemia; Broca, 1861). At the

183 time, Broca did not dissect the brains of his patients, therefore he was not able to know that

184 their lesions extended far into neighboring regions and the white matter (Dronkers et al. 2007).

185 The posterior portion of the inferior frontal gyrus was soon termed Broca's (Fig. 1) area and

186 early language models considered it a speech-related brain region primarily supporting

187 language production (Green 1970; Goodglass, Gleason, and Hyde 1970; Weigl and Bierwisch

188 1970). Further lesion studies associated the left superior temporal gyrus with language

189 comprehension abilities (Wernicke 1874). Jointly, these observations gave rise to the

190 Wernicke-Lichtheim-Geschwind (WLG) model of the neurobiology of language in which

191 Broca's area subserves language production and so-called Wernicke's area (roughly left

192 posterior superior temporal gyrus) enables language comprehension (Geschwind 1970;

193 Lichtheim 1884). Although the WLG model correctly identified two major nodes in the

194 language network, the model's anatomical assertions are nowadays severely underspecified,

195 with incorrect functional attributions and impoverished linguistic description (Friederici, 2011;

196 Hagoort, 2014; Tremblay & Dick, 2016).

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198   Insert Figure 1 here

199

200 **3. The early days: Neuropsychological evidence for syntax in the brain**

201 Before the advent of functional neuroimaging, studying patients with brain lesions as well as

202 patients undergoing neurosurgical interventions such as, for example, a corpus callosotomy

203 (i.e. a split-brain operation) were the only way in which relationships between brain structure

204 and cognitive functions could be established. Patients provided researchers with "natural

205 experiments" that made it possible to draw inferences regarding the cognitive function

206 supported by the destroyed tissue, given a patient's observed behavioral deficit or lack thereof

207 due to a vascular disease (stroke), a brain contusion (accident) or after a surgical intervention.

208 In line with the ideas of the WBL model mentioned above, traditional classifications of aphasic

209 syndromes pay little attention to linguistic theory and instead tend to classify patients with

210 regard to the loss of their language production or comprehension abilities. The loss or deficit

211 of language production abilities is usually termed Broca's aphasia, whereas the loss or deficit

212 of language comprehension abilities is labelled Wernicke's aphasia. We will here strictly focus

213 on studies that are relevant to the neuroscience of syntax and abstain from discussing

214 aphasiology and aphasic syndromes in any detail (see Raymer & Rothi, 2015 for a general

215 overview).

216 Zurif, Caramazza and Myerson (1972) were the first to suggest that the aphasic syndrome

217 leading to Broca's aphasia was not merely a language-production or speech-related deficit, as

218 suggested by the WBL model in which Broca's area subserves language production and

219 Wernicke's area supports language comprehension. Following linguistic theorizing of

220 language competence to be distinct from performance, Zurif and colleagues, reasoned that a

221 competence deficit should affect performance both in production and comprehension. In their

222 seminal work, the authors used a grammatical judgement task asking patients classified as

223 Broca's aphasics—a subgroup of which usually exhibit behavior that is labelled as

224 "agrammatic" in the literature—to sort words from a set of sentences on the basis of how

225 closely related they thought the words would be. Zurif and colleagues found that the structures

226 that the aphasic patients sorted excluded almost systematically all those grammatical elements

227 (function words) that were not necessary part of the intrinsic meaning of the sentence, while

228 retaining major lexical items. The authors thus concluded that "since the agrammatic aphasic's

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229   tacit knowledge of English syntax appears to be as restricted as is his use in syntax, we may

230   presume that agrammatism reflects a disruption of the underlying language mechanism".

231   Caramazza and Zurif (1976) tested Broca's aphasics' comprehension further, using center-

232   embedded sentences that could be correctly understood either on the basis of semantic

233   constraints ("the apple that the boy is eating is red"; semantically, only the boy can eat the

234   apple, not vice versa), or on the basis of syntactic relationships among words ("the man that

235   the woman is hugging is happy"; semantically, both the man and the woman can hug the other,

236   while syntactically, only the woman can hug the man). Again, the authors found that Broca's

237   aphasics performance dropped to chance when they had to use syntactic information. Thus,

238   they proposed that these patients suffered from an impairment specifically related to "syntactic-

239   like cognitive operations" in language comprehension *and* production caused by damage to the

240   brain's "anterior language area" (i.e. Broca's area). A similar point of view was echoed by

241   Friederici (1981) and Friederici, Schönle, and Garrett (1982) who asserted that the deficit in

242   agrammatic Broca's aphasics can be described as the inability of patients to assign syntactic

243   structure.

244   The repeated association of agrammatic Broca's aphasia with frontal lesions led Grodzinsky

245   (2000) to eventually put forward the so-called trace-deletion hypothesis. This hypothesis

246   constituted a first attempt at establishing explicit links between an aphasic syndrome (Broca's

247   aphasia), a brain region (Broca's area), and a specific linguistic theory (Government-and-

248   Binding theory; Chomsky, 1988). More precisely, the central claim of the trace-deletion

249   hypothesis was that Broca's area implements cognitive functions that relate to the movement

250   of phrasal constituents, but only with regard to noun phrases and wh-phrases, excluding head-

251   movement. Grodzinsky thus considered the impairment of Broca's aphasics to be related to

252   one very particular aspect of linguistic theory, whereas the general ability to build phrases or

253   for syntactic processing construed more broadly was thought be preserved in these patients.

254   While recent development within the Minimalist framework challenge the trace-deletion

255   hypothesis at the theoretical level (Nunes 2011), the very coarse neuroanatomical precision of

256   the lesion areas due to vascular diseases is a clear downside of aphasia studies. Moreover, the

257   notion of "Broca's area" has been defined in many different ways by different researchers

258   (Tremblay & Dick, 2016). Today, Broca's area is understood to be neither

259   cytoarchitectonically nor functionally homogenous (Amunts & Zilles, 2012; Goucha &

260   Friederici, 2015; Hagoort, 2013; Hagoort & Indefrey, 2014; Zaccarella, Schell, & Friederici,

261   2017; Zilles & Amunts, 2018). Against this background, the general observation that lesions

262   are rarely focal and tend to encompass more than just one particular brain region becomes even

263   more damping. More recent work in aphasiology has tried to overcome some of these

264   limitations using a so-called lesion-symptom mapping approach relying on the overlap of many

265   individual lesions (for a review see Wilson, 2017) but the general reservations still hold.

266   In sum, lesion studies have been a reliable tool for establishing first brain-behavior

267   relationships, showing that syntactic abilities are lateralized and, to an extent, depend on the

268   posterior portion of the inferior frontal gyrus in the language dominant hemisphere. But

269   mapping linguistic computations onto neural circuitry requires an approach that captures the

270   computational machinery of the human language faculty in more parsimonious and generic

271   (i.e. minimalist) terms and, at the same time, provides a much more fine-grained assessment of

272   the involved neural structures on the neuroscientific side. The advent of structural and

273   functional neuroimaging has provided researchers with a tool capable of obtaining such fine-

274   grained data which we can attempt to link to linguistic computations.

4. Functional imaging of syntactic computations

First support to the existence of a neural syntactic component building-up hierarchical linguistic structures can be found in neurocognitive approaches that use on-line parsing algorithms based on grammatical information metrices, to test neural behavior correlating with linguistic competence during actual performance (Brennan 2016). Albeit different methodologies employed across the studies, such approaches have begun to show that hierarchy-based syntactic algorithms (Brennan et al. 2016; Nelson et al. 2017; Bhattasali et al. 2019; Brennan and Hale 2019) 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[1].

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: (i) the universal principles of grammar by means of possible and impossible syntactic rules; (ii) the brain's adherence to hierarchical constituency; (iii) movement; (iv) the degree of recursion; (v) the *Merge* computation. Overall, syntactic processing appears to be strongly localizable in the left hemisphere, including Broca's region, and specifically in BA44, the posterior superior temporal gyrus (pSTG) and the superior

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[1] Although beyond the scope of the present review, convergent evidence for a primarily role of hierarchical processing in language comes from very recent neural oscillation findings, which showed that cortical activity at different timescales tracked the time course of abstract linguistic structures at different levels (words, phrases and sentences), thus driving the internal construction of hierarchical linguistic structure during listening to connected speech (Ding et al. 2016; also see Martin and Doumas 2017).

293   temporal sulcus (pSTS; Friederici, 2011; Hagoort & Indefrey, 2014; Zaccarella, Schell, &

294   Friederici, 2017). Here we discuss some few representative functional studies testing syntax in

295   the brain. This list of study is by no means intended to be exhaustive, but it tries to broadly

296   cover some of the most central issues on natural language syntax tested using functional

297   imaging in the mature brain.

298   In a seminal study comparing possible and impossible grammars, Musso and colleagues had

299   German native speakers learn sets of grammatical rules of Italian and Japanese

300   languages which could either be real or unreal in the sense that they would violate general

301   syntactic principles of human grammar (Musso et al. 2003). Subjects would either learn a

302   language that, for example, used lexical elements from real Italian and required a linguistic

303   parameter setting different from the subjects' native German (e.g., the null-subject parameter:

304   *Mangio la pera.,* literally "eat the pear" with the meaning "I eat the pear"), or a language that

305   used lexical elements from real Italian but relied on an impossible rule (e.g., negation being

306   established by arbitrarily emphasizing the linear position of a word in the sequence instead of

307   using hierarchy: *Paolo mangia la no pera.*, literally "Paolo eats the no pear"). The authors

308   report a change of activation in Broca's area throughout the course of the functional

309   neuroimaging study, with an increase of activation in later runs (when presumably subjects

310   have mastered novel rules) relative to earlier runs (when presumably subjects are still learning

311   the rules). Critically, this increase only occurred for languages with rules that agreed with

312   structure-dependent rules of universal grammar as posited in generative grammar, and not for

313   languages with rules that depended on linear order and not structure. The same patterns of data

314   in Broca's region had been also reported when different stimuli and population samples were

315   tested, still manipulating real and impossible syntactic rules (Tettamanti et al., 2002).

316   The neural adherence to hierarchical constituency has been first tested by Pallier and colleagues

317   using fMRI to measure neural activity correlating with constituent size of linguistic structures

318   (Pallier, Devauchelle, and Dehaene 2011). Specifically, subjects were asked to read sequences

319   of 12 words or pseudowords, which could form constituents of 12-word length ("I believe that

320   you should accept the proposal of your new associate"), or being decomposed in smaller

321   constituents of reduced size, like 6 ("the mouse that eats our cheese; two clients examine this

322   nice couch"), 4, 3, or 2 while lying in the scanner. The authors found a set of areas in the left

323   posterior temporal and inferior frontal regions, including Broca's area, showing constituent

324   size effects regardless of whether the constituents were formed by real content words, or

325   whether they were replaced by pseudowords. This suggests that these areas are able to access

326   abstract syntactic frames to build well-formed constituent structures, even in the absence of

327   semantic meaning. On the other hand, regions in the temporal pole, anterior superior temporal

328   sulcus and temporo-parietal junction showed constituent size effect only in the presence of real

329   content words.

330   The linguistic concept of *movement* describes word order permutations by having

331   discontinuous constituents or displacements within a sentence (see Nunes 2011 for a re-

332   definition of Movement in Minimalist terms). A study by Ben-Shachar et al. (2003) in Hebrew

333   and found that movement could be localized in the left inferior frontal gyrus (i.e. Broca's area)

334   and in the pSTS and suggested that the structural analysis of sentences containing syntactic

335   movement may take place in Broca's area, while access to predicate argument structure might

336   occur in the left pSTS. Friederici et al. (2006) showed that the activation in the posterior portion

337   of Broca's area (BA 44) parametrically increased as the number of moved constituents

338   increased. In this study activation was also found in the posterior temporal cortex though this

339   activation did not change with the number of moved constituents.

340 Functional studies on recursion have been motivated by the attempt to test how human brain

341 might handle grammars of increasing generative power, ranging from low-level AB^n finite-

342 state grammars (FSG) based on transitional probabilities, to more complex A^nB^n phrase-

343 structure grammars (PSG) that can generate structures of natural human languages. In one first

344 artificial grammar fMRI experiment, Friederici and colleagues could show that the two

345 grammars are supported by different areas in the human brain, such that the FSG processing is

346 subserved by the left frontal operculum, while the posterior portion of Broca's area (BA 44), a

347 phylogenetically younger cortical area, appears to be specifically active during the computation

348 of PSG dependencies (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006). In a second

349 experiment using a natural grammar and German sentences as stimuli, PSG rules generating

350 double-embedding structures ("Maria, [die Hans, [der gut aussah], liebte], Johan geküsst

351 hatte]"; *Maria who loved Hans who was good looking kissed Johan*) also revealed activation

352 in BA44 driven by syntactic complexity operationalized as the number of embedded sentences

353 (Makuuchi, Bahlmann, Anwander, & Friederici, 2009). The latter study in contrast to the

354 former study, using natural meaningful sentences additionally activated the posterior superior

355 temporal cortex (Friederici et al., 2006).

356 In recent years, different imaging studies have begun to reduce stimulus complexity to very

357 basic two or three-word levels to determine the localization of single applications of merge in

358 the human brain (Schell, Zaccarella, & Friederici, 2017; Zaccarella & Friederici, 2015;

359 Zaccarella, Meyer, Makuuchi, & Friederici, 2015). By using determiner phrases with very

360 reduced conceptual content consisting of a function word and a pseudoword (*Diese Flirk;* This

361 flirk), it was possible to localize *Merge* in a very confined subpart of the most anterior-ventral

362 BA44 with little variance across subjects. List strings without any function word, which in

363 contrast only involved the frontal operculum/anterior insula (Zaccarella & Friederici, 2015)—

364 a phylogenetically older part of the cortex (Sanides 1962; Amunts and Zilles 2012). Thus, these

365 results converge on the idea that Broca's area is involved during syntactic processing, with

366 specific neural populations of BA44 being especially active during *Merge* application, be it at

367 very basic levels or more complex ones.

5. Functional and structural connections of the syntactic network

369 At the functional level, methods of analysis estimating the directionality of information flow

370 between specific regions during experimental stimulation (Dynamic Causal Modeling, DCM;

371 Friston, Harrison, & Penny, 2003) has made it possible to observe how regions active for

372 syntactic tasks might co-work during phrase structure building. One first study found that

373 syntactic complexity—operationalized as complex object-cleft vs. less complex subject-cleft

374 sentences—appears to be primarily processed in the IFG—which acts as a pure syntactic

375 processor—and then sent to the pSTS/STG, which seems to rather support verb argument

376 structure (den Ouden et al. 2012). The centrality of the IFG as the driving input for syntax has

377 been confirmed by further studies using either complex object-first sentences (Makuuchi &

378 Friederici, 2013) , or very simple two-word phrases (Wu, Zaccarella, and Friederici 2019), thus

379 suggesting IFG's primary role in phrase structure building independently of hierarchical

380 complexity (Fig. 2). Worth noting is the observation that activity in BA44 and in the pSTS/STG

381 during language experiments have been found to correlate with each other already when

382 modulatory effects driven by linguistic manipulations are removed from the signal, indicating

383 the existence of a basic network acting as a general framework for language processing

384 (Lohmann et al. 2010).

385

386 Insert Figure 2 here

387   At the structural level, diffusion tensor imaging (DTI) has made it possible to identify structural

388   connections between brain regions in vivo (Catani and Thiebaut de Schotten 2008), thus

389   revealing distinct dorsal and ventral white matter fiber bundles connecting the inferior-frontal

390   with posterior temporal regions (Fig. 3). The dorsal pathway linking the posterior Broca's area

391   (BA44) with the posterior temporal cortex via the arcuate fascicle has been demonstrated to

392   correlate with the ability to perform syntactic processes (Friederici et al., 2006; Skeide et al.,

393   2016; Wilson et al., 2011). Further evidence in this respect comes from structural data based

394   on probabilistic tractography, which show that the activation peak in BA44 obtained from the

395   PSG artificial grammar paradigm based on nonadjacent hierarchical dependences (A^nB^n)

396   connects with the pSTG along the dorsal pathway. Results from DTI-based tractography

397   propose that the ventral pathway linking BA47 and anterior Broca's (BA45) to the temporal

398   cortex via the extreme fiber capsule system rather supports semantic processing (Saur et al.

399   2008).

400   Overall, the precise neuroanatomical characterization of the linguistic network implementing

401   syntax makes it possible to ask whether this network is already present at birth and how it

402   develops during maturation (ontogeny), as well as whether this network is present in the brains

403   of non-human primates and how it evolved (phylogeny). These neuroscientific questions and

404   their purported answers are directly related to Chomsky's insight that crucial aspects of the

405   syntactic component are innate as well as the hypothesis that it is unique to our species. These

406   issues will be discussed in turn in the two following sections.

407

408   Insert Figure 3 here

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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 & 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 no involvement of the inferior-frontal regions above the statistical threshold (Skeide, Brauer, & Friederici, 2014). Only around the end of the 10th year of life children begin to approach first syntax-specific responses in the left IFG. BA44 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 BA45. Notably, another functional study could further show that increased neural activity in the left temporal regions—and to a lesser extent in BA44—can already be appreciated in five years 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 3 years of age to young adulthood (Skeide, Brauer, & Friederici, 2015). Collectively, these findings suggest that the neural resources for the development of syntactic

434 knowledge initially primarily recruit the posterior superior temporal cortex, and only later they

435 shift towards BA44 as a function of age and proficiency.

436 When looking at changes in functional connectivity between pSTG and Broca's area, the

437 coordination between these two regions as observed in the mature brain during speech and

438 language processing only develops gradually from early infancy to adulthood (Dehaene-

439 Lambertz, Dehaene, and Hertz-Pannier 2002; Perani et al. 2011). Whereas the adult brain

440 exhibits a marked lateralization and intrahemispheric functional connectivity between Broca's

441 area and pSTG, newborns show interhemispheric connectivity between these regions in the left

442 hemisphere and their respective right-hemipsheric homologues, mainly between the superior

443 temporal regions (Friederici, Brauer, & Lohmann, 2011). The mature pattern of lateralization

444 and increased functional connectivity between Broca's area and left pSTG can only be

445 observed at around 6 years of age when using task-free measures such as resting-state fMRI

446 (Xiao, Friederici, Margulies, & Brauer, 2016), thus indicating that maturation of the core

447 language network ultimately leads to an increased specialization and functional segregation of

448 the processing of semantic and syntactic information (Skeide, Brauer, & Friederici, 2014).

449 Investigations into the anatomical development of brain functions, including language, move

450 from the fact that while brain function relies on the transmission of electrical impulses from

451 one brain region to another via white-matter pathways, the efficiency of information

452 transmission is determined by the degree of myelination of a particular fiber tract (Nave and

453 Werner 2014; Wake, Lee, and Fields 2011). Different fiber tracts in the human brain exhibit

454 distinct developmental trajectories as evidenced by their different degrees of myelination

455 during maturation (Dubois et al. 2008; Lebel et al. 2012; 2008; Pujol et al. 2006). Crucially,

456 the dorsal fiber tract connecting pSTG to BA 44 develops rather late during childhood and its

457 degree of myelination is highly predictive for a child's capacity to process hierarchically

458   complex sentences (Brauer, Anwander, & Friederici, 2011; Skeide, Brauer, & Friederici, 2016;

459   Skeide & Friederici, 2016). Conversely, the dorsal pathway targeting premotor cortex and the

460   ventral pathway targeting BA 45 and more anterior portions of the inferior frontal gyrus area

461   already well myelinated early on in life and thus highly functioning (Fig. 4). These pathways

462   support phonological learning during early infancy (Friederici, Mueller, & Oberecker, 2011;

463   Kuhl et al., 2006). As a matter of fact, analyses of the cortical microstructure measuring the

464   volume of cell bodies in Broca's area indicate that leftward asymmetry in BA44 is only visible

465   around the age of 11 years, whereas leftward asymmetry of BA45 is already present much

466   earlier around 5 years of age (Amunts, Schleicher, Ditterich, & Zilles, 2003). Taken together,

467   the maturation of the structural network including BA44 in the IFG dorsal connection to the

468   posterior temporal cortex appear to be crucial to the mastering of syntax processing in natural

469   language.

470   Insert Figure 4 here

471   The initially weak structural integrity of the core language network raises the question as to

472   how this relatively late maturation for complex syntax might nonetheless enable young children

473   to begin mastering more basic merging combinations. Behavioral studies put forward the

474   hypothesis that very young children might already be able to produce determiner-noun

475   combinations ("the cat" or "a cat"), by freely combining determiners and nouns according to

476   syntactic rules (Yang 2013), even in case of sensory-deprivation due to deafness and lack of

477   systematized linguistic input (Goldin-Meadow and Yang 2017). Neural evidence further

478   supports the idea that very young children might be already able to detect local phrase structure

479   violations in the linguistic stream (Bernal et al. 2010; Brusini et al. 2016). One open possibility

480   is that linguistic processing during early childhood might primarily depends on the pathways

481   targeting the ventral connections to the IFG in order to allow for basic structure building (i.e.

482   a single application of Merge). In contrast, the processing of structurally more complex, non-

483   canonical and embedded structures requires additional working memory resources and is

484   therefore dependent on more dorsal portions of Broca's area (Makuuchi, Bahlmann, Anwander,

485   & Friederici, 2009) and the dorsal pathway which also provides a link to inferior parietal

486   regions involved in verbal working memory (Fengler, Meyer, and Friederici 2016; L Meyer et

487   al. 2012; Grossman et al. 2002). Another possibility is that syntactic processing effects are

488   difficult to detect with fMRI due to the fact that they rely on a relative as opposed to an absolute

489   baseline: According to Chomsky's more recent ideas about language acquisition, the vast

490   majority of the acquisition process may actually be dedicated to acquiring lexico-semantic

491   knowledge and externalization procedures specific to the target-language (Berwick &

492   Chomsky, 2016). This is in line with the observed developmental trajectory of the structure

493   and function of the core language network which we have discussed here and implies that

494   primarily lexico-semantic processing in posterior temporal cortex initially overshadows

495   syntactic processing effects in inferior frontal regions on the neural level, whereas behavioral

496   data clearly indicate a strong reliance on syntactic knowledge already early in life.

497   **7. Phylogeny**

498   From an evolutionary point of view, the neural mechanisms for syntactic structure building

499   could have evolved in non-human species either via evolutionary convergence with an only

500   distantly related species (e.g., songbirds), or by descent from a common primate ancestor

501   (Bolhuis et al. 2014). Despite these principled reasons and continuous efforts to discover

502   homologies of human language in non-human primates, there is so far no empirical evidence

503   that any non-human species has evolved a system with the computational capacity exhibited

504   by the human syntactic system (Beckers et al. 2012; Berwick et al. 2013; 2011; Bolhuis,

505   Okanoya, and Scharff 2010; Bolhuis et al. 2014; Yang 2013). Given that the comparative

506 method has been the standard approach to the study of language evolution a potentially

507 demoralizing conclusion follows, and namely that if language is specific to the human species

508 then there actually may be "not much to compare" (Bolhuis et al., 2014).

509 This holds the more so as a recent study analyzing the brain's white matter structure in hearing

510 subjects and early deaf signers revealed a separation of the neural network for language and

511 vocal speech (Finkl et al. 2019). While no group difference was found the language network,

512 significant differences were found for the speech-related network, thereby providing evidence

513 for a separation between language and speech as postulated by Chomsky (Chomsky, 1995;

514 Chomsky, 2005; Friederici et al., 2017).

515 The fact that we now have a solid neuroanatomical characterization of the core language

516 network that subserves syntactic processing in humans invites cross-species comparisons to go

517 beyond behavioral studies which have compared the performance of humans and non-human

518 primates on comprehension and production tasks involving symbol combination and sequence

519 processing (for a review see Friederici, in press). So far, all studies comparing the performance

520 of humans and non-human primates on comprehension and production tasks involving symbol

521 combination and sequence processing converge on the fact that non-human primates lack

522 systematic combinatorics as they do not approach the ability of processing hierarchical

523 sequences that go beyond linear combinations (Fitch and Hauser 2004; Hauser, Chomsky, and

524 Fitch 2002).

525 This conclusion holds up independent of the modality of language use and can therefore not be

526 attributed mechanisms for vocal learning, as the use of sign language stimuli in studies with

527 non-human primates has yielded similar results (Terrace et al. 1979; Yang 2013). Converging

528 on the conclusions, comparative functional neuroimaging studies have shown that the learning

529   of linear sequences in non-human primates and humans differentially recruited frontal cortex

530   in an interesting pattern, and namely that while macaques showed activation in the homologue

531   to Broca's area—the ventral frontal opercular cortex—in response to simple forward-branching

532   violations, neural activation in response to violations in humans was found in the frontal

533   operculum in the ventral frontal cortex but not in Broca's area (Wilson et al., 2015). As

534   monkeys appear to be able to learn non-hierarchical rules-based rules, this has been suggested

535   to be a possible phylogenetic precursor of phrase-structure processing in humans, and a

536   possible cross-correspondence with language development in children (Friederici, 2017).

537   The functional differences in the recruitment of frontal cortex during sequence processing and

538   the apparent inability of non-human primates to process hierarchically structured phrases are

539   also evidenced in differences with regard to brain structure and connectivity across species

540   which parallel the immaturity of this network in humans in infancy. Cortical terminations of

541   the arcuate fasciculus as the fiber pathway connecting Broca's area and pSTG in humans differ

542   considerably between humans and non-human primates (Rilling et al., 2008; Perani et al.,

543   2011). Moreover, cytoarchitectonic analyses reveal that, compared to humans, non-human

544   primates like chimpanzees exhibits no leftward asymmetry, either in BA45 or in BA44

545   (Schenker et al. 2010). This regional asymmetry in humans compared to non-human primates

546   is accompanied by a strong asymmetry of the arcuate fasciculus itself (Rilling, Glasser, Jbabdi,

547   Andersson, & Preuss, 2012; Rilling et al., 2008; Rilling, 2014), thus pointing towards the view

548   that dorsal fiber tract connecting BA44 to the pSTG/STS might constitute a crucial

549   neurological precondition for linguistic humaniqueness—the capacity of handling hierarchical

550   linguistic structures—to take place along evolution (Goucha, Zaccarella, and Friederici 2017).

551

8. Conclusion

In the present chapter we discussed neuroanatomical evidence supporting humans' capacity to handle linguistic hierarchies. We moved 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 judgements 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 BA44 and posterior temporal cortex along the dorsal fiber track. We provide first 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., 2006); 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

576 stages of the dorsal pathway for the mastering of syntax processing in natural language (Skeide

577 & Friederici, 2016). We concluded with the hypothesis that the dorsal fiber tract connecting

578 BA44 to the pSTG/STS might constitute a crucial neurological precondition for our capacity

579 of handling hierarchical linguistic structures to emerge (Goucha, Zaccarella, and Friederici

580 2017).

581 We would like to end up this chapter with a reflection on the legacy that Chomsky's ideas have

582 had on the neuroscience of language. Such legacy is according to us essentially twofold: the

583 view of language as a biological system which is implemented in the human brain, and the idea

584 that grammar and performance factors do not equate each other. These two aspects, we believe,

585 are necessarily subsumed in any study approaching language in experimental settings. Such

586 experimental approaches, on the other side, have proven to offer first empirical validation for

587 the biological validity of core claims about the human capacity for language , as put forward

588 in generative grammar and within the minimalist framework. More importantly, these present

589 experimental results clearly call for increased collaboration between linguists and

590 neuroscientists is highly desirable to bring the relation between linguistic phenomena and

591 neural data to a deeper level of understanding (Friederici & Singer, 2015; Poeppel, 2012).

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597 **Conflicts of interest**

598 None of the authors has conflicts of interest to declare.

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Figure captions

Figure 1: Cortical regions of the linguistic 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 BA47. 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 (BA41/BA42), the superior temporal gyrus (STG) (BA22), the middle temporal gyrus (MTG) (BA21) and BA37 as well as the anterior temporal pole (BA38).

Figure 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 BA44 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. Adapted from Wu, Chiao Yi, Emiliano Zaccarella, and Angela D. Friederici. 2019. "Universal Neural Basis of Structure Building Evidenced by Network Modulations Emerging from Broca's Area: The Case of Chinese." Human Brain Mapping 40 (6): 1705–17. DOI:10.1002/hbm.24482.

Figure 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. Adapted from Goucha, Tomás, Emiliano Zaccarella, and Angela.D. Friederici. 2017. "A Revival of Homo Loquens as a Builder of Labeled Structures: Neurocognitive Considerations." *Neuroscience and Biobehavioral Reviews* 81 (Pt B): 213–24. DOI:10.1016/j.neubiorev.2017.01.036.

**Figure 4: Ontogeny of the 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). Newborns show only the pathway to the premotor cortex. Adapted from Perani, Daniela, Maria C Saccuman, Paola Scifo, Alfred Anwander, Danilo Spada, Cristina Baldoli, Antonella Poloniato, Gabriele Lohmann, and Angela D Friederici. 2011. "Neural Language Networks at Birth*." Proceedings of the National Academy of Sciences of the United States of America* 108 (38): 16056–61. DOI:10.1073/pnas.1102991108.

Cortical regions of the language network
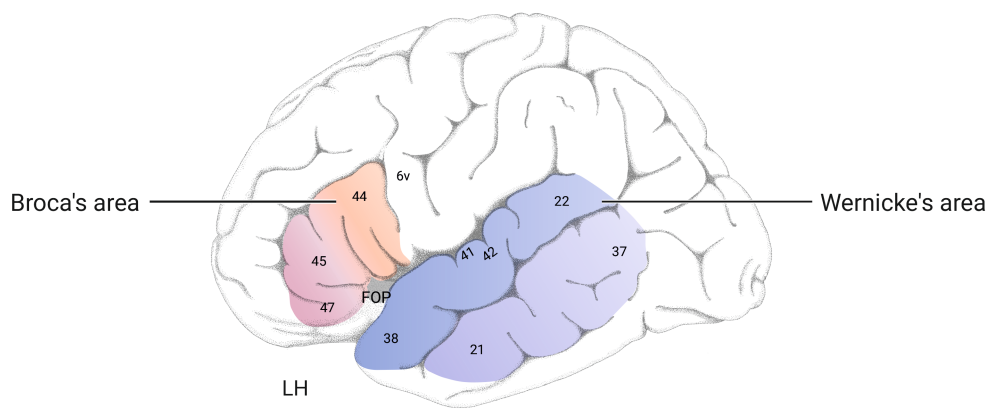
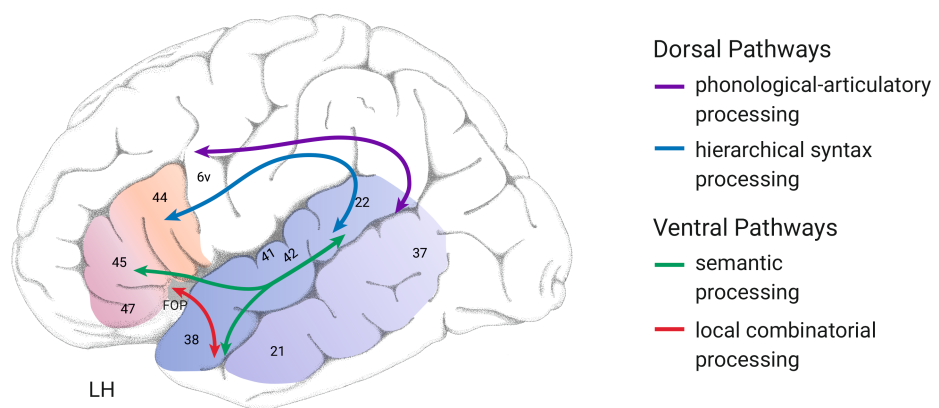# Driving input for syntax in the left posterior inferior frontal gyrus
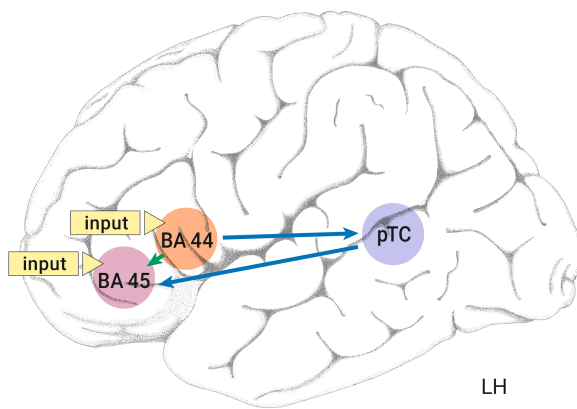
Phrasal combination

1st word	2nd word		Noun
這 (this)	張 (CL)	+	桌子 (table)

— increased connectivity modulation

— decreased connectivity modulation

LH

adapted from Wu, Zaccarella and Friederici, 2019

Ventral and dorsal pathways for language

Dorsal Pathways

— phonological-articulatory processing

— hierarchical syntax processing

Ventral Pathways

— semantic processing

— local combinatorial processing

adapted from Goucha, Zaccarella and Friederici, 2017

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)