

The Neurobiology of Syntax

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1 Introduction

Despite the relative ease of use for most people, language represents a complicated assortment of interacting computations and representations needed to map between an idea and a physical signal and back again. Dating back to the 19th century, there has been general agreement that the storage and computational needs of language are subserved by a specialized language network in the brain couched in the frontal, temporal, and parietal lobes (Geschwind, 1970; Nasios et al., 2019). This network is comprised of broad swaths of cortex and corresponding white matter pathways—organized into a dorsal and a ventral stream—which facilitate functional interactions between the relevant regions to carry out both the production and comprehension of language (Hickok and Poeppel, 2000, 2004, 2007; Kümmerer et al., 2013). The gray matter regions and corresponding pathways that comprise the “high-level” language network are fairly agreed upon in the literature as a largely left-lateralized fronto-temporal network (Friederici, 2011; Regev et al., 2021, although see Schneck et al. (2021) for exceptions).¹ This high-level cortical network also appears to interact with the basal ganglia and other subcortical structures to carry out the requisite computations (Barbas et al., 2013; Moreno et al., 2018; Murphy et al., 2022a). The language network is functionally specified (Skeide et al., 2016; Braga et al., 2020; Hiersche et al., 2022), and functionally differentiated for its different sub-functions (at least in some accounts; Friederici et al., 2003; Uddén et al., 2022). This network is remarkably consistent across individuals (Fedorenko et al., 2010; Mahowald and Fedorenko, 2016; Scott et al., 2017; Lipkin et al., 2022), even appearing to hold across diverse spoken languages (Malik-Moraleda et al., 2022). It has also been found that the same network carries out linguistic operations even across language modalities—spoken, written, or signed (Neville et al., 1998; Sakai et al., 2005; Newman et al., 2015; Moreno et al., 2018; Arana et al., 2020; Liu et al., 2020; Trettenbrein et al., 2021; Matchin et al., 2022c).

In the rest of this paper, I will first discuss the mainstream neurobiological models of syntax, followed by the kinds of approaches that are used in the literature to probe syntactic competences. I will then go region-by-region and discuss the evidence for or against the role of that region in syntactic computation. Admittedly, not all of the regions presented feature prominently in the mainstream models, however they still generated enough work to warrant discussion. I finish by revisiting the major conceptual models with some discussion of their parsimony with the empirical data.

2 Neurobiology of syntax

Within this high-level language network, the areas which underlie hierarchical syntactic computation and representation remain hotly debated. The language sciences as a whole have not yet

¹Because of the consistent left-lateralized findings in the literature, when regions are discussed below, they can be assumed to be in the left hemisphere unless otherwise specified.

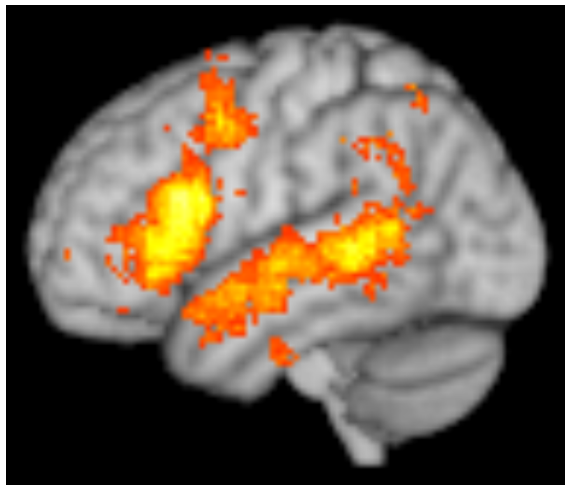
converged on an agreed-upon definition of syntax. In this work, we will consider syntax to be the abstract hierarchical relationships between lexical items in language based on their structural properties rather than their semantic or phonological ones. Even the concept of a *lexical item* remains controversial, as what constitutes a word is not consistent across languages (Haspelmath, 2017). While these debates around what constitutes syntax or a lexical item are crucial to creating a complete model of the language system, they are best addressed elsewhere. Instead I have restricted my review to works which make specific claims about the neurobiological localization of syntactic functions, without focusing too much on the nature of these computations and representations. A challenge in all of this is delineating the distribution of labor between syntax and the lexicon (Bates and Goodman, 1997; Fedorenko et al., 2012b; Rezaii et al., 2022; Le Normand and Thai-Van, 2022), and between syntax and semantics (Skeide et al., 2014; Pykkänen, 2016).

Broadly speaking, the suspects in the case for the missing syntax center are the Inferior Frontal Gyrus (IFG), the anterior temporal lobe (ATL), posterior temporal lobe (PTL), inferior parietal lobe/ angular gyrus (AG), the white matter tracts connecting these regions, or all of them together. To illustrate the lack of consensus (or perhaps the absence of a more refined locus), Figure 1a shows a meta-analysis from Neurosynth for fMRI studies which carried out “syntactic” manipulations in their experiments (Yarkoni et al., 2011). The activation across the entire higher-level language system does little to pare down our suspects.

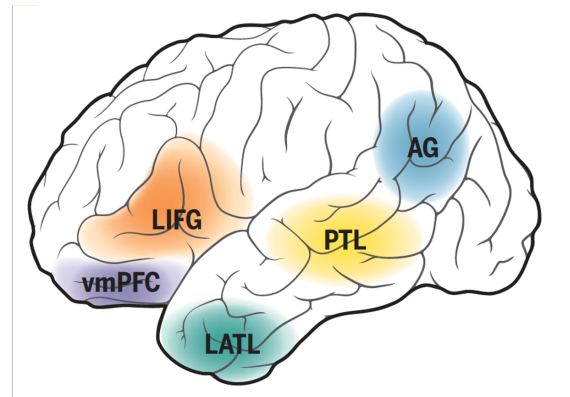
On this backdrop, there are five mainstream models for the neurobiology underlying syntax in the brain (labeled for their main proponents): Fedorenko, Friederici, Pykkänen, Hagoort, and Matchin & Hickok. In all of these models, there exists some interaction between posterior temporal areas and inferior frontal ones via the dorsal and/or ventral white matter tracts, but the nature of these interactions and the kinds of information and computations undertaken differ in important ways.

2.1 Fedorenko

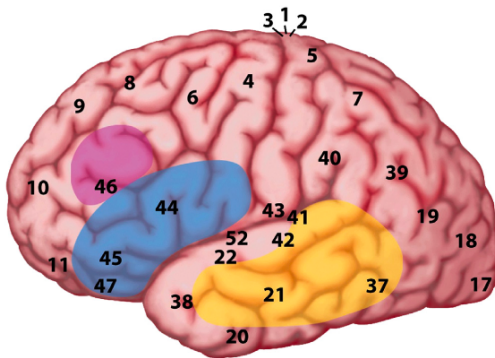
The first theoretical proposal is that of Fedorenko et al. (2020). In this work, the authors carried out a series of fMRI studies wherein they identified individual functional regions of interest (fROIs; Fedorenko et al., 2010; Fedorenko, 2021) on the basis of a sentences vs. non-word lists contrast. They then gave their participants three tasks designed to tap into syntactic processing in contrast to lexical-semantic processing. Within the individual fROIs, they do not find any region which responds more to their syntactic manipulations than their lexical ones. They thus argue that no region within the language network is specialized for any kind of syntactic operation, but the whole network more broadly supports meaning rather than form.



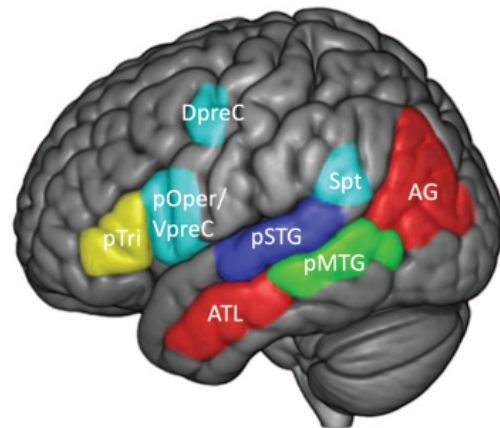
(a)



(b)



(c)



(d)

Figure 1: (a) Meta-analytic association test map for the term “syntactic”. (b) Pylkkänen’s proposed combinatory network. LATL (left anterior temporal lobe) and vmPFC (ventromedial prefrontal cortex) support conceptual combinatorics; AG underlies argument structure; LIFG is sensitive to long-distance dependencies; PTL carries out potentially syntactic combinatory operations. Reproduced from Pylkkänen (2019). (c) Hagoort’s MUC framework. “Memory” areas are in yellow, “Unification” areas are in blue, and “Control” areas are in magenta. Reproduced from Hagoort (2016). (d) Matchin and Hickok’s proposed structure. Red regions (ATL & AG) underlie conceptual-semantic processing; green region (pMTG) supports hierarchical lexical-syntactic processing; yellow region underlies linear morpho-syntactic processing. Reproduced from Matchin and Hickok (2020).

2.2 Friederici

The next theoretical proposal is that of Zaccarella and Friederici (2017). They argue for a differentiated fronto-temporal language network wherein the Pars opercularis of the IFG underlies the Minimalist Program’s Merge operation (Chomsky, 2014) in two steps—string Merge, and hierarchy Merge (Zaccarella and Friederici, 2015; Zaccarella et al., 2017b; Zaccarella and Friederici, 2017). This hub—which performs both forward and backward mappings between linear sequences and hierarchical structures—will then build syntactic structures, supported by storage in the inferior parietal lobe (Meyer et al., 2012). They argue that the role of the posterior temporal lobe is thematic assignment—a semantic operation (Friederici et al., 2009; Zaccarella et al., 2017a).

2.3 Pykkänen

Pykkänen (2019) proposes a combinatorial network which underlies semantic and syntactic combinatorics in language (Figure 1b). This larger combinatorial network comprises the ATL, AG, IFG, and PTL. While they lay out a clearer picture of the semantic combinatorial network—in ventromedial prefrontal cortex, anterior temporal lobe, and angular gyrus—they decline to make strong claims about the syntactic network apart from that a) it is distinct from the semantic combinatorial system, b) structure-based (although not necessarily syntactic) processing occurs in PTL, and c) the IFG is probably involved with long-distance dependencies. They do stipulate, however, that in comprehension, only the semantic composition is carried out, as the syntactic composition is unnecessary.

2.4 Hagoort

The next model is that of Hagoort (2016) which provides additional details on the Memory, Unification, Control (MUC) model (Figure 1c; Hagoort, 2003, 2005a,b, 2013, 2014, 2019). Within this model, syntactic frames associated with individual lexical items are unified into a structural representation of the utterance. The lexical items and syntactic frames are posited to be stored in and retrieved from the posterior temporal lobe (the Memory component of the model), whereas the Unification takes place in the inferior frontal lobe (Hagoort, 2017). This unification operation is used in both production and comprehension, and across the morphological, semantic, and syntactic (and even non-linguistic) domains. Within this model, however, no region is truly functionally specified, but rather serves different functions depending on which functional network it is operating as a part of. Furthermore, all higher-level linguistic computation is posited to take place in the “Unification space” in the IFG.

2.5 Matchin & Hickok

The final model, that of Matchin and Hickok (2020), proposes that syntax is divided into two components in production: hierarchical lexical-syntactic processing which takes place in pMTG, and linear morpho-syntactic sequencing which takes place in the Pars triangularis of the IFG (Figure 1d). These regions are differentially recruited in production and perception, however. In perception, the IFG serves as a “mental rewind button”, whereas in production it serves as a mapping between hierarchical representations (from pMTG) and linear morpho-syntactic sequences. By contrast, pMTG does both forward and backward mapping of hierarchical structures.

3 Empirical data collection

Despite the best efforts of the scientific community, it is so far impossible to *directly* observe the syntactic system at work—it isn’t possible to just look into a brain and see a neuron putting together a syntactic tree. As such, the field has devised a number of creative methods and paradigms to indirectly observe or tap the system. Most of the works cited in this review are based on functional neuroimaging studies using functional Magnetic Resonance Imaging (fMRI; Buckner et al., 1996; Bandettini, 2012), Magnetoencephalography (MEG), or intracranial electroencephalography (iEEG) or electrocorticography (ECoG). Within the fMRI literature, there is increasing attention in recent years to the fact that the same functions may not be located in *exactly* the same place for all individuals in a study. For this reason, it can be useful to employ a functional localizer to identify relevant functional regions of interest (fROIs) on a different task in order to hone in on the relevant regions across participants in analysis (Fedorenko et al., 2010, 2012c).

Another approach to localize the syntactic system is to use lesion-symptom mapping wherein patients with focal brain damage are observed or submitted to tests in order to establish a causal relationship between behavioral or linguistic deficits and the locus of the lesion (Bates et al., 2003; Matchin and Rogalsky, 2017; Wilson, 2017). Lesion-symptom mapping can be especially informative in the context of specific syntactic impairments like paragrammatism (Kleist, 1914; Butterworth and Howard, 1987) and agrammatism (although these two conditions remain relatively poorly defined; see Matchin et al., 2020, for a review). Broadly construed, agrammatism is characterized by “telegraphic” speech which omits functional morphemes in lieu of short lists of content words. By contrast, paragrammatism is often characterized by long utterances with more than necessary morpho-syntactic structure, and deficits in the hierarchical organization of sentences (Matchin et al., 2020).

A variety of experimental paradigms are used to probe syntactic abilities and processing in the literature. One of the most common experimental paradigms is to contrast unstructured lists of words to well-formed sentences, supposing that the only difference between the sentences and the lists of words is the presence of hierarchical structure. A particular instantiation of this is the

composition of two-word phrases (e.g.: *the car* or *blue trucks*) compared to two-word expressions that cannot be combined into a well-formed phrase (Pylkkänen and Brennan, 2019). This contrast would therefore isolate the processing of syntactic structure—and indeed seems to—in studies of neural oscillations which were found to synchronize to phrase and sentence level rhythms in hierarchical but not scrambled sentences (Brennan and Hale, 2019; Lo et al., 2022).

Unfortunately, syntax is not the only difference between well-formed sentences and word lists. In addition to being more complex in structure than word lists, sentences encode relational meaning. In order to sidestep this shortcoming of the basic sentences vs. word lists paradigm, researchers have attempted to construct well-formed sentences devoid of meaning by replacing the content words with non-words but keeping the function words in place—often referred to as jabberwocky (based on Carroll, 1872). The idea here is that Jabberwocky “sentences” contain syntactic structure but lack coherent lexical meaning and can therefore be compared to word lists without the semantic confound (Matchin and Wood, 2020).

Another tool to sidestep participants’ linguistic knowledge and isolate syntax is to use artificial grammar learning tasks (Petersson and Hagoort, 2012). In these studies, participants are presented with a toy grammar which (usually) employs either a hierarchical phrase-structure grammar, or a simpler non-hierarchical one (e.g.: $A^n B^n$ nested grammar). Indeed, these artificial grammars can be learned quickly, making them useful for experimental settings (Getz et al., 2018), however there is also evidence that participants are recruiting other strategies to succeed in the grammar learning tasks (De Vries et al., 2008). There are also observations that artificial grammar learning paradigms activate a network which overlaps with—but is not the same as—the language network (Uddén and Männel, 2018).

Yet another paradigm used to hone in on syntax is that of contrasting simple sentences with more complex ones—usually involving movement or complex argument structure. A drawback of this technique, however, is that the more complex sentences often entail greater working memory demands than their simpler counterparts which represents a confound when trying to isolate syntactic processing (Rogalsky et al., 2008). There are also claims that the argument structure manipulations tap more into the semantic system than the syntactic one (Malyutina and den Ouden, 2017).

An approach to avoid these task-related confounds exists in the form of naturalistic language comprehension paradigms. In these experiments, participants are presented with linguistic stimuli (most commonly an audiobook; Futrell et al., 2017; Bhattasali et al., 2020; Nastase et al., 2021), and then computational estimates of linguistic complexity are correlated with the neural signal (Brennan, 2016; Li and Hale, 2019). These tasks have the advantage of being (more or less) neutral in terms of task demands, and that multiple questions and regressors can be used to examine a single dataset. They are, however, much less tightly controlled and constrain the kinds of questions that can be asked, requiring substantial linguistic and computational resources to be used effectively.

It should be noted that most of the work with healthy participants focuses more on syntactic comprehension than production, which in some cases results in a very strong assumption: that the same system subserves both syntactic comprehension and production. Furthermore, it has been shown that different tasks tap into different neural resources, thus underscoring the need for a variety of data types rather than the use of a small set of paradigms (Dronkers et al., 2004; Caplan et al., 2016). Another drawback of the existing literature is that it is primarily conducted on English, and if not English, then another European language. Again, there is a need for diversification as studies carried out in different languages can yield different results (Xu et al., 2020).

I now turn to the general anatomical regions that are often cited for their role in syntactic processing.

4 Inferior Frontal Cortex

The first (and most popular) candidate for the cortical seat of syntax is the Inferior Frontal Gyrus (IFG). The IFG is most often pointed to as the seat of language (including syntax) since Paul Broca’s famous case in the 19th century (Broca, 1861a,b). Although historically thought to support general speech production needs (Geschwind, 1970), it has since been shown to be active in perception as well. The IFG is divided into three parts—Pars orbitalis, Pars triangularis, and Pars opercularis—which correspond roughly to Brodmann Areas (BA) 47, 45, and 44 respectively. The sub-regions of the IFG also present different connectivity patterns (Xiang et al., 2010). There is little doubt that the IFG has a role in the language network (Hickok and Poeppel, 2004, 2007; Fedorenko et al., 2010; Mahowald and Fedorenko, 2016; Scott et al., 2017), however its precise role in the system and to what extent it subserves perception and/or production, particularly of syntax, remains under debate.

4.1 Broca’s Area

The exact boundaries of Broca’s area remain a topic of debate (Tremblay and Dick, 2016), but a common operationalization is that it constitutes BAs 44 & 45 (although some studies just use IFG and Broca’s area interchangeably). Notwithstanding, there is no shortage of studies claiming that Broca’s area constitutes the brain’s syntax computation center in some form or another.

From the functional neuroimaging literature, many studies have found greater activation in Broca’s area in conditions with greater syntactic complexity. Such activation has been found in studies which contrast lists of words to sentences (Brennan and Pytkänen, 2012; Matchin et al., 2017; Uddén et al., 2022), simple sentences with more complex ones like object vs. subject relatives (Constable et al., 2004; Thompson et al., 2010), noun-phrase vs. complementizer phrase embedding (Shetreet et al., 2009), movement (Makuuchi et al., 2013; Shetreet and Friedmann, 2014; Europa et al., 2019), argument structure (Meltzer-Asscher et al., 2015), datives vs. intransitives (Allen

et al., 2012), and passive vs. active sentences (Mack et al., 2013). This region has been shown to adapt to repeated syntactic structures (Segaert et al., 2012; Hanna et al., 2013), and to respond to syntactic interference (Glaser et al., 2013). Broca’s area involvement has also been shown in response to anomalous sentences—but not predictable ones—in patients with primary progressive aphasia (PPA; Tyler et al., 2009).

Another group of studies has found Broca’s area activation to correspond to the rhythms of higher-level structures such as phrases or sentences (Ding et al., 2016; Sheng et al., 2019, although see Frank and Yang (2018); Kalenkovich et al. (2022) for an alternative explanation). The amplitude of Broca’s area activation has also been found to correlate with constituent length (Pallier et al., 2011; Nelson et al., 2017; Chang et al., 2020). In a similar vein, activity in Broca’s area has been found to correlate with the actions or predictions of computational parsing models pointing to a role for Broca’s area in syntactic parsing or tree-building (Ohta et al., 2013; Brennan et al., 2016; Henderson et al., 2016; Bhattasali et al., 2018, 2019; Brennan et al., 2020).

Within artificial grammar learning studies, Broca’s area has been found to be more heavily involved and to demonstrate a different connectivity pattern in sequence processing of “real” linguistic rules (i.e.: rules derived from real grammatical rules in natural language) compared to unreal ones (Musso et al., 2003) or to a phrase-structure grammar compared to a finite-state grammar (Friederici et al., 2006). It is also implicated in a study of word category learning (Weber et al., 2019). A similar pattern was found when contrasting the activity of a group of participants trained on the artificial grammar with an untrained group (Chen et al., 2019).

Damage to the IFG can also be informative to its role in syntactic processing. Mesulam et al. (2015) found that damage to the IFG—alongside damage to a handful of temporal sites—resulted in impaired comprehension on syntactically complex items on the Northwestern Assessment of Verbs and Sentences (NAVS; Cho-Reyes and Thompson, 2012; Thompson et al., 2013). It has also been implicated in plausibility judgment accuracy (Graessner et al., 2021). PPA patients with left frontal atrophy presented with deficits in syntactic processing (Wilson et al., 2016). Even temporary “lesions” to the IFG induced by transcranial magnetic stimulation (TMS; Sliwiska et al., 2014; Weise et al., 2020) have been found to impact behavior on syntactic tasks, particularly in resolving syntactic ambiguities (Acheson and Hagoort, 2013; Meyer et al., 2018), but also in grammaticality judgments in an artificial grammar (Uddén et al., 2017).

The IFG is also shown to be engaged in both production and perception processes, but is differentially recruited for each (Giglio et al., 2022). On the production side, patients with stroke-induced damage to the IFG presented with expressive agrammatism (Matchin et al., 2020, 2022a), and patients with PPA damage to the same region had persistent syntactic errors in production (Wilson et al., 2010b). In a stimulation study, (Chang et al., 2018) found that stimulating sites in the IFG resulted in syntactic (but not word-finding) deficits. Furthermore, the involvement of the IFG has been found to show distinct grammatical responses during production in intracranial EEG

(Sahin et al., 2009). It is also recruited in the production of grammatical determiners (Ishkhanyan et al., 2020).

Following from these various experimental findings, a variety of specific syntactic computations have been posited for the IFG. Such functions include word order processing (den Ouden et al., 2012; Hultén et al., 2019), integration of words into constituents (Maran et al., 2022), incremental phrase processing and integration (Hagoort, 2005b; Snijders et al., 2009; Nelson et al., 2017; Uddén et al., 2022; Stanojević et al., 2021), morphosyntax (den Ouden et al., 2019), dependency structures (Grodzinsky and Friederici, 2006; LOVE et al., 2008; Leiken et al., 2015; Lopopolo et al., 2021), generalized sequence processing (Petersson et al., 2012), syntactic movement (Mack et al., 2013), syntactic knowledge (Pylkkänen, 2019), syntactic prediction (Matchin et al., 2017; Hartwigsen et al., 2017; Wang et al., 2018) (but see Heilbron et al. (2022) for a null prediction effect in IFG), hierarchical tree construction and analysis (Friederici, 2004; Pattamadilok et al., 2016), and even as the central hub of linguistic computations (Trettenbrein et al., 2021). The Hagoort model takes Broca’s area to be the seat of Unification space, carrying out unification operations across domains (Hagoort, 2013).

A problem with any of the above accounts, however, is that Broca’s area does not represent a single, architectonically consistent region (Anwander et al., 2007; Amunts et al., 2010; Amunts and Zilles, 2012, 2015; Zilles and Amunts, 2018; Fedorenko and Blank, 2020), with observations that not the whole of Broca’s area is sentence-selective (Rogalsky et al., 2015) and in fact some parts of the area are not specialized for language at all (Fedorenko et al., 2012a; Papitto et al., 2020). This has led to proposals that rather than supporting a single type of computation, multiple domain-general and language-specific processes are couched in Broca’s area (Boeckx et al., 2014; Kunert et al., 2015; Matchin, 2018; Fahey and den Ouden, 2020). There are, however, other proposals that speak directly to sub-parts of the IFG. It also bears noting that the effects observed and attributed to Broca’s area are probably attributable to effects more localized to the sub-parts of the IFG.

4.2 IFG: Pars triangularis

A number of studies have found results specifically regarding the Pars triangularis (IFG_{tri}; BA 45), including greater activation in response to (more complex) sentences than simpler ones or word lists (Kinno et al., 2008; Rogalsky et al., 2015; Zaccarella et al., 2017a), differential responses to nouns and verbs (Strijkers et al., 2019), and the development of syntactic deficits in Primary Progressive Apraxia of Speech patients following atrophy of IFG_{tri} (Whitwell et al., 2017). Amici et al. (2007) found that damage to IFG_{tri} specifically impacted embedded sentence comprehension in patients with neurodegenerative disease. These results have led to proposals for the role of IFG_{tri} similar to those above for Broca’s area as a whole. (Wu et al., 2019) propose that IFG_{tri} is responsible for processing lexico-semantic information, whereas (Quiñones et al., 2018) propose that IFG_{tri} underlies the computation of grammatical or dependency relations, or that it supports syntactic

prediction in online comprehension (Santi and Grodzinsky, 2012; Jakuszeit et al., 2013; Matchin et al., 2014). Within the Matchin and Hickok (2020) model, IFG_{tri} serves as a translator between hierarchical structures in PTL and linear morpho-syntactic sequences in production.

4.3 IFG: Pars opercularis

The Pars opercularis (IFG_{oper}; BA 44) has also been targeted as the seat of syntax. A number of artificial hierarchical grammar learning fMRI studies have found activation for both artificial and natural grammars in IFG_{oper} (Bahlmann et al., 2008; Tagarelli et al., 2019; Chen et al., 2021a,b), including artificial grammars with long-distance dependencies, the processing of which is considered a keystone of syntactic competence (Opitz and Friederici, 2007). Studies using relatively simple sentences with content words replaced by jabberwocky have also found activation here (Friederici et al., 2000; Matchin and Wood, 2020), even after controlling for derivational morphology (Goucha and Friederici, 2015).

Functional imaging studies targeting complex syntax have also found activation in IFG_{oper}. Such manipulations included syntactic reframing (Stromswold et al., 1996; Dapretto and Bookheimer, 1999) (although see Siegelman et al. (2019) for a failed replication of this result), contrasting verb- and noun-phrases using the same words (Matchin et al., 2019b), embedded & non-canonical word order sentences (Wilson et al., 2010a; Meyer and Friederici, 2016), and long-distance verb-argument relations (Kuhnke et al., 2017). Studies targeting phrase structure building have implicated the IFG_{oper} in processing (Grodzinsky and Friederici, 2006; Meyer et al., 2012; Hagoort and Indefrey, 2014; Schell et al., 2017) as well as syntactic working memory (Fiebach et al., 2005). It has also been found that damage to this region impacts processing of complex syntax (Wilson et al., 2010a; Meyer and Friederici, 2016), and reduces overall syntactic complexity in production (Gleichgerricht et al., 2021).

It has thus been posited within the Friederici account that IFG_{oper} is the seat of the Merge operation (Chomsky, 2014), either on its own (Friederici, 2018, 2020) or in coordination with posterior temporal structures (however maintaining that the computational legwork happens in BA44; Zaccarella and Friederici, 2015; Zaccarella et al., 2017a,b; Wu et al., 2019).

4.4 IFG Counterpoints

Despite these findings, however, there are some critical issues with the proposal that the IFG is requisite for the processing of hierarchical syntax. In response to proposals that the IFG (or its subparts) underlie hierarchy-building operations domain-generally, Martins et al. (2019) find that the IFG does not show any activation during a hierarchical motor-sequencing task (but see Zaccarella et al., 2021, for a review). While this does not necessarily mean that the IFG does not support this function in language, it constrains the possibilities of its function. Another issue is that this region has been found to correlate with linguistic rhythms even in the absence of

syntactic structure (Ten Oever et al., 2022), begging the question of whether the region is doing something hierarchical or simply tracking rhythms in language. Another issue is that there is inconsistent evidence as to whether the IFG supports production and perception or just one or the other (Walenski et al., 2019).

Some more incriminating evidence comes from the clinical literature where it has been found that damage to the IFG does not predict impaired performance in a sentence comprehension task (Dronkers et al., 2004; Thothathiri et al., 2012), or in acute stroke prior to functional reorganization (Sheppard et al., 2022). This has led to the proposal that activation of the IFG during such tasks is simply a confound of task demands (Rogalsky et al., 2008, 2018; Leiken and Pylkkänen, 2014; Kunert et al., 2015; Matar et al., 2021). Even in healthy participants, tasks targeting syntax do not necessarily activate it (Matchin and Hickok, 2016), and if they do, such activation does not necessarily hold across methods (Matchin et al., 2019a). Hierarchical psycholinguistic language models are also inconsistent in providing predictions for activity in this region (Hale et al., 2015). Furthermore, it had long been held that damage to the IFG should cause Broca’s aphasia, a condition with severe productive syntax deficits, however damage to the IFG is not sufficient to induce Broca’s aphasia (Turken and Dronkers, 2011; Gajardo-Vidal et al., 2021; Andrews et al., 2023). This collection of results has led to proposals that the white matter tracts connecting the IFG to the temporal lobe—rather than the IFG itself—are necessary for hierarchical processing (see Section 8 below; Fridriksson et al., 2007; Mesulam et al., 2015; Fridriksson et al., 2018).

5 Anterior Temporal Cortex

The next candidate region for the seat of syntax is the Anterior Temporal Lobe (ATL). This region can be further subdivided into the Temporal Pole (TP) and the anterior Superior Temporal Gyrus (aSTG), but many papers refer to the entire region simply as ATL. This region has repeatedly been implicated in studies of composition with different proposals to its specific function (Pylkkänen and Brennan, 2019).

Several studies have argued that because this region activates more in response to expressions with internal structure compared to those without (e.g.: sentences vs. word lists), then it is the seat of syntactic composition (Bemis and Pylkkänen, 2011, 2013; Brennan and Pylkkänen, 2012; Blanco-Elorrieta et al., 2018) or is a crucial node in the combinatorial network (Pylkkänen, 2019). Activity in ATL appears to show adaptation to syntactic structures (e.g.: active vs. passive sentences, Segaert et al., 2012), respond selectively to higher-level processes in sentences and phrases (Sheng et al., 2019), and to respond to syntactic contrasts in jaberwocky studies (Friederici et al., 2000).

Activity in the ATL has been found to correlate with higher-level linguistic predictors in naturalistic studies. Such predictors include the number of open nodes/steps in a parse tree (Brennan et al., 2012), surprisal estimates derived from context-free treebank grammars (Hale et al., 2015; Henderson et al., 2016), left-corner parsing steps for hierarchical grammars (Brennan et al., 2016;

Brennan and Pyllkänen, 2017), and bottom-up parser actions (Bhattachali et al., 2018, 2019). Some of these predictors correspond to activity only in this area, while others implicate ATL as part of a larger network (Allen et al., 2012).

ATL has also been argued to correlate with syntactic performance in aphasia. Magnusdotir et al. (2013) found that damage to ATL (as well as other temporal structures) corresponded to poorer performance on a sentence-picture matching task. Mesulam et al. (2015) found that damage to a number of fronto-temporal structures, among them the ATL, correlated with poorer comprehension of difficult items from the NAVS (Cho-Reyes and Thompson, 2012; Thompson et al., 2013), and Graessner et al. (2021) found that damage to the ATL was related to decision speed in a plausibility judgment task.

There also exist specific claims as to the ATL’s role in syntactic processing within the larger language network. Grodzinsky and Friederici (2006) propose that the aSTG supports local phrase structure processing in interaction with the IFG. Lopopolo et al. (2021) similarly propose that the ATL specifically processes dependency structures alongside the IFG. Stanojević et al. (2021) propose that the ATL does time-locked combinatorics, incorporating linguistic elements in real time, while other parts of the language network function to consolidate these pieces into more efficient structures.

Because the region also activates in semantic contrasts, there have been proposals that it is the seat of both semantic and syntactic composition (Rogalsky and Hickok, 2009), however the view that the ATL is the seat of syntax has largely fallen out of favor, having been replaced by proposals that it is more so the site of semantic memory (Binder et al., 2009; Binder and Desai, 2011) or semantic composition (Westerlund and Pyllkänen, 2014; Westerlund et al., 2015; Zhang and Pyllkänen, 2015; Pyllkänen, 2016, 2020; Flick and Pyllkänen, 2020). This claim is supported by arguments that many of the experimental paradigms used to probe syntax are actually probing semantic composition (Malyutina and den Ouden, 2017). Further evidence is provided by neuroimaging studies which do not show (or do not replicate) ATL involvement in syntactic tasks (Uddén et al., 2022; Matchin and Hickok, 2016; Matchin et al., 2019b), as well as findings that ATL lesions do not result in syntactic deficits (Kho et al., 2008; Wilson et al., 2012, 2014b; Rogalsky et al., 2018; Stark et al., 2019).

6 Posterior Temporal Cortex

Apart from the IFG, the posterior temporal lobe (PTL) has most often been cited as the seat of language processing, including syntax. This is where Wernicke’s area is found, on the posterior part of the superior temporal gyrus (STG; Wernicke, 1874). Such findings citing the PTL include its involvement in sentence comprehension (complex or otherwise; Thompson et al., 2010; Thothathiri et al., 2012; Brennan and Pyllkänen, 2012; Wilson et al., 2016; Matar et al., 2021), grammaticality judgments (Wilson and Saygin, 2004), production as well as perception (Walenski et al., 2019),

and tracking constituent length (Chang et al., 2020) or parsing steps (Brennan et al., 2016, 2020; Pylkkänen, 2019), although activity did not appear to correlate with syntactic surprisal (Henderson et al., 2016). These data have led to proposals that the PTL subserves the integration of a word into the sentence (Zaccarella et al., 2017b; Hultén et al., 2019), or the computation of grammatical or dependency relations (Quiñones et al., 2018). Within the Hagoort model, the PTL is proposed to store lexico-syntactic information (Hagoort, 2013).

Much like the IFG, however, the posterior temporal lobe is not a single region but rather can be divided into three relevant parts: the STG, the superior temporal sulcus (STS), and the middle temporal gyrus (MTG). Admittedly, though, the boundaries can be a bit fuzzy (Tremblay and Dick, 2016).

6.1 Posterior Superior Temporal Gyrus

Within the posterior temporal lobe, a large number of studies have made claims specifically about the superior temporal gyrus (pSTG). This region has been found to track the phrasal (but not lexical or sublexical) rhythm when listening to speech (Ding et al., 2016; Sheng et al., 2019), as well as to be more sensitive to structured phrases or sentences than word lists (Glaser et al., 2013; Williams et al., 2017), and seems to be sensitive to syntactic processing demands like phrase length (Hagoort and Indefrey, 2014; Nelson et al., 2017) or anomalous structures (Kinno et al., 2008; Herrmann et al., 2009; Tyler et al., 2009; Flick and Pylkkänen, 2020). The involvement of the pSTG in syntactically demanding operations has been made on the basis of studies showing greater activation in conditions involving embeddings (Constable et al., 2004) or movement (Shetreet and Friedmann, 2014; Pattamadilok et al., 2016; Europa et al., 2019). Activity in pSTG has been shown to correlate with hierarchical phrase-structure parser predictions (Bhattasali et al., 2018; Lopopolo et al., 2021; Stanojević et al., 2021), as well as with part-of-speech predictions (Heilbron et al., 2022). It has thus been proposed that the pSTG is responsible for the online construction and manipulation of hierarchical phrase structures. This proposal is coherent with findings from the artificial grammar learning literature finding that the pSTG is more responsive to hierarchical phrase-structure grammars than nested ones (Chen et al., 2019, 2021a), and underlies word category learning (Chen et al., 2021b). Another group of proposals suggest that the pSTG is responsible for verb-argument (Thompson et al., 2007; den Ouden et al., 2012, 2019; Allen et al., 2012) or dependency structure (Frankland and Greene, 2015) relations.

These proposals from the functional neuroimaging literature have varying degrees of parsimony with clinical findings regarding damage to the pSTG. Such damage has been found to correlate with comprehension deficits in non-canonical sentences (Mesulam et al., 2015; Fridriksson et al., 2018; Kristinsson et al., 2020), paragrammatic production (Yagata et al., 2017; Matchin et al., 2020), and fluency disruptions (Wilson et al., 2010b).

6.2 Posterior Superior Temporal Sulcus

Just below the STG is the superior temporal sulcus (pSTS). While fewer studies have focused specifically on this region compared to the gyri neighboring it, it has been shown to be responsive to many of the same phenomena. In particular, activity in the pSTS has been found to correlate with constituent size (Pallier et al., 2011), argument structure (Matchin et al., 2019b), phrase structure (Matchin et al., 2017; Murphy et al., 2022b), thematic role assignment (Frankland and Greene, 2015), and grammatical disambiguation (van der Burght et al., 2019). In fact, when TMS is applied to this region, participants rely more heavily on semantic rather than syntactic cues for disambiguation (Kyriaki et al., 2020). It has been shown to be sensitive to syntactic complexity supramodally (Wilson et al., 2018; Matchin et al., 2022c) and argued to be activated by the Merge operation due to its role in thematic assignment within the Friederici framework (Zaccarella et al., 2017a).

6.3 Posterior Middle Temporal Gyrus

Continuing downward, we arrive at the Middle Temporal Gyrus (pMTG). Activation in the pMTG has repeatedly been shown in contrasts focused on syntactic structure vs. a lack thereof (Makuuchi et al., 2013; Williams et al., 2017; Wu et al., 2019; Matchin and Wood, 2020), embedded sentences (Shetreet et al., 2009), or other kinds of syntactic complexity manipulations in both comprehension (Kinno et al., 2008; Tyler et al., 2009; Uddén et al., 2022) and production (Takashima et al., 2020), although differentially recruited for the two processes (Giglio et al., 2022). It is also shown to be activated by the processing of hierarchical artificial grammars (Friederici et al., 2006), and to correlate with syntactic surprisal (Lopopolo et al., 2017) or computational parser actions (Bhattasali et al., 2019) in naturalistic paradigms. Claims have also been made that the pMTG instead underlies semantic integration rather than syntactic (Meyer and Friederici, 2016), however it appears to be more sensitive to syntactic ambiguities than semantic ones (Rodd et al., 2010). Damage to the pMTG has also repeatedly been shown to result in impaired comprehension, particularly to more syntactically complex items (Turken and Dronkers, 2011; Tyler et al., 2011; Pillay et al., 2017; Kristinsson et al., 2020; Matchin et al., 2022a), as well as paragrammatic production (Matchin et al., 2020). It has thus been proposed that the pMTG functions as the hub of a syntactic network (Schoffelen et al., 2017; Yu et al., 2022), as well as the storage site of lexical-syntactic information (Snijders et al., 2009). There is also evidence that the pMTG plays a crucial role in the storage of the lexicon (Hickok and Poeppel, 2004, 2007) which is consistent with observations from TMS (Krieger-Redwood and Jefferies, 2014) or aphasia (Dronkers et al., 2004) that lesions to the MTG impair lexical access. As such, there are proposals that the pMTG serves as the interface between the lexicon and syntax (Bozic et al., 2015; Weber et al., 2019; Caucheteux et al., 2021). In the Matchin and Hickok (2020) model, the pMTG supports hierarchy building by both storing treelets in the lexicon, as well as combining or decomposing them.

7 Inferior Parietal Lobe

Posterior to the temporal lobe lies the inferior parietal lobe, in particular the angular gyrus (AG). As this region consistently shows activation in syntactic complexity manipulations (usually involving sentence-level contrasts; Constable et al., 2004; Shetreet et al., 2009; Shetreet and Friedmann, 2014), it has also become a suspect in this case. It has been argued to support phrase (but not sentence) composition (Williams et al., 2017), and support verb-argument processing (Thompson et al., 2007; Meltzer-Asscher et al., 2015; Malyutina and den Ouden, 2017; Takashima et al., 2020), although recall that Malyutina and den Ouden (2017) argue that verb-argument processing taps into the semantic system rather than the semantic one. This is consistent with observations of the AG supporting thematic role assignment (another semantic task; Mack et al., 2013; Quiñones et al., 2018), and semantic integration (Price et al., 2015; Schell et al., 2017), and serves as an important node in semantic memory Binder et al. (2009); Binder and Desai (2011).

8 White Matter Tracts

While the above sections have focused on gray matter regions, another group of accounts suggests that syntactic competence relies rather on the white matter tracts connecting gray matter regions (Petersson and Hagoort, 2012; Friederici, 2018). A set of crucial details has been omitted from the sections above: as none of them operates in a vacuum they all have both input and output connectivity to other cortical regions (Xu et al., 2020). The two main white matter tracts connecting inferior frontal and posterior temporal regions are the arcuate fasciculus (AF) and superior longitudinal fasciculus (Yagmurlu et al., 2016), although the connections between these regions are more intertwined than simply these two tracts (Baboyan et al., 2021). These tracts are more developed in modern humans than our nearest relatives (Sierpowska et al., 2022), and their development correlates with language performance in human children (Skeide et al., 2016; Friederici, 2020). Damage to the connections between inferior frontal cortex and posterior temporal cortex has been shown to correlate with productive (Fridriksson et al., 2007; Gajardo-Vidal et al., 2021; Gleichgerrcht et al., 2021; Matchin et al., 2022b) or receptive (Griffiths et al., 2013; Fridriksson et al., 2018; Sheppard et al., 2022) syntactic deficits, or both (Wilson et al., 2011; Bonakdarpour et al., 2019; den Ouden et al., 2019), even when controlling for neighboring gray matter damage. While they may not be the seat of the computations, it does seem that the connections between posterior temporal and inferior frontal regions are crucial for a fully functioning language system in both production and perception. Within each of the mainstream models, these connections play an important role between storage and computational regions (Hagoort, 2016; Zaccarella and Friederici, 2017; Pylkkänen, 2019; Fedorenko et al., 2020; Matchin and Hickok, 2020).

9 Distributed Networks

The last group of accounts does not take syntax to be situated in any one particular location in the language network, but rather as a computation carried out by a distributed network of regions (Fedorenko and Thompson-Schill, 2014). Interacting with the language network (but separable from it; Blank et al., 2014) is the Multiple Demand (MD) network that has often been shown to be active during language tasks (Wilson et al., 2008; Matar et al., 2019). Because the MD network carries out computations supporting other neural systems, it has been proposed that it supports syntactic computation, however there is substantial evidence that the MD network does not carry out any language-specific computations (Blank and Fedorenko, 2017; Shain et al., 2020; Diachek et al., 2020; Ryskin et al., 2020; Quillen et al., 2021; Wehbe et al., 2021, see Fedorenko and Shain (2021) for a review). Blank et al. (2016) and Fedorenko et al. (2020) found that subjects’ individually localized language networks showed distributed responses to syntactic complexity manipulations, leading to arguments that the language system is undifferentiated for syntax. One of the main proposals regarding this largely undifferentiated language network relies on neural oscillations (Poeppel, 2014). Indeed, such oscillations (especially in the alpha and lower-beta frequency bands; Bastiaansen et al., 2010; Kielar et al., 2015) have been found in response to syntactic manipulations (Ding et al., 2016; Fedorenko et al., 2016; Zhang and Ding, 2017). Contra the Fedorenko proposal, however, there is evidence that these oscillations function differently for lexical and syntactic processes (Segaert et al., 2018; Vassileiou et al., 2018)

10 Discussion

I now return to the mainstream models in the literature. I have included Figure 2 for ease of reference, as much for myself as for the reader.

10.1 Fedorenko

Again, Fedorenko et al.’s claim is that the language system is undifferentiated between lexical and syntactic demands (Blank and Fedorenko, 2019; Hu et al., 2022). Instead, the lexical system draws on a distributed network, and syntax is just incidental to meaning composition. As such, syntactic deficits in aphasia are simply the result of “economy of effort” (Fedorenko et al., 2022). While it is clear that higher-level language draws on a widely distributed network, and even some syntactic functions appear to be broadly distributed (Wilson and Saygin, 2004; Bautista and Wilson, 2016), the assertion that the syntactic system simply does not exist does not stand up to the data, especially as their claim is based almost exclusively on fMRI data. The main counterargument to this claim is that it does not explain why damage to different parts of the cortex results in different syntax-related syndromes like paragrammatism vs. agrammatism (Matchin et al., 2020) or the

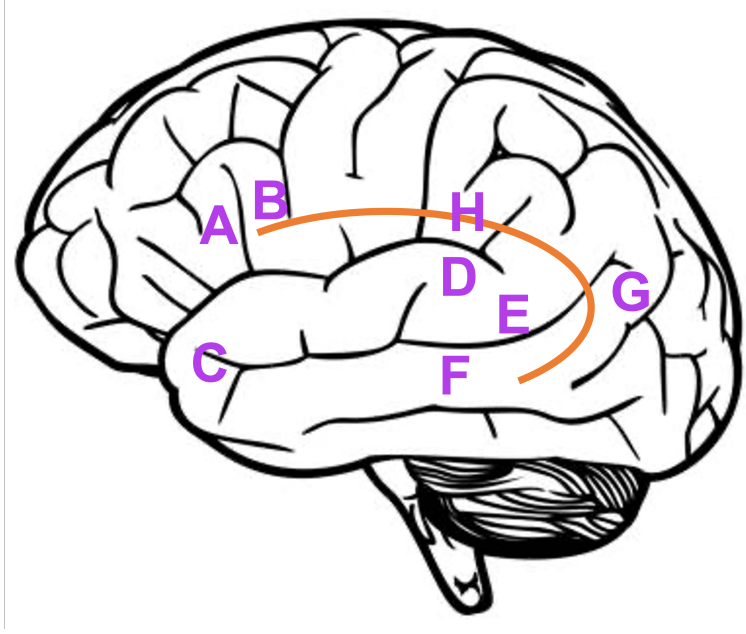


Figure 2: Rough schematic of the left-hemispheric higher level language network. **A** = IFG_{tri}, **B** = IFG_{oper}, **C** = ATL, **D** = pSTG, **E** = pSTS, **F** = pMTG, **G** = AG, **H** = Arcuate fasciculus.

differential morphosyntactic deficits observed across subtypes of PPA (Wilson et al., 2014a) or in TMS (Kroczeck et al., 2019).

10.2 Friederici

The Friederici proposal is, in essence, that IFG_{oper} (B in Fig. 2) carries out all of the syntactic computations required in a two-step Merge operation—string Merge, and hierarchy Merge (Zaccarella and Friederici, 2017). They posit that the role of the posterior temporal lobe (D, E in Figure 2) is thematic assignment. This proposal, too, fails to account for the clinical data. They suggest that Broca’s aphasia and corresponding agrammatic output are a result of damage to the Merge center. The problem, however, is that damage to IFG_{oper} is neither necessary nor sufficient to induce Broca’s aphasia (Fridriksson et al., 2007, 2015; Andrews et al., 2023), nor does damage to Broca’s area result in an agrammatic comprehension pattern (Rogalsky et al., 2018). Furthermore, this model does not explain paragrammatic output. It is also important to note that posterior temporal lobe involvement has been shown in artificial grammar learning paradigms, casting doubt on its semantic role (Uddén and Männel, 2018).

10.3 Pylkkänen

As far as syntax is concerned, the Pylkkänen model posits a structural combinatory hub in the posterior temporal lobe (D, E, F in Fig. 2), and that the IFG (A, B) is implicated in long-

distance dependencies. Given the largely underspecified nature of the proposal, these facts are broadly consistent with the data, but fall short of providing much explanatory insight into syntactic processing.

10.4 Hagoort

Within the Hagoort model, lexical and syntactic frame information is stored in the posterior temporal lobe (E, F in Fig. 2) which is communicated via the arcuate fasciculus (H) to the IFG (A, B) where it is manipulated in the Unification space (Hagoort, 2013, 2017; Weber et al., 2019). While the multimodal nature of the IFG for unification does have some empirical support (Rodd et al., 2010; Kunert et al., 2015), this account would predict that damage to the IFG would have devastating effects for both productive and receptive syntax, as creating a full parse of a hierarchical structure would be impossible. Here too, the model does not stand up to the clinical data: patients with inferior frontal damage often have expressive language problems, but not receptive ones—an asymmetry that is not well accounted for in this model.

10.5 Matchin & Hickok

Matchin and Hickok’s proposal has the highest degree of parsimony with the empirical data. Under this model, the IFG_{tri} (A in Fig. 2) supports morpho-syntactic linearization processes in production, while pSTG and pMTG (E, F) underlie both the storage of syntactic treelets and their manipulation in both production and comprehension. This distribution of labor better accounts for the observations from both the clinical and functional neuroimaging literatures. Their position regarding the morphosyntactic role of the IFG is supported by the observation that the IFG is involved in the production of grammatical determiners (Ishkhanyan et al., 2020), and its implication in expressive agrammatism (Matchin et al., 2020, 2022a), a condition partially characterized by the frequent or complete omission of functional morphemes. In the same way, their proposal regarding the role of the posterior temporal lobe is consistent with the patterns observed in paragrammatism and some varieties of PPA, wherein greater comprehension deficits are observed, and morphosyntax is used, but in an often unprincipled way (Wilson et al., 2012; Matchin et al., 2020).

11 Conclusions

Despite the abundance of experiments addressing the question, the neurobiological underpinnings of syntax remain elusive and contentious. There is general consensus about the regions implicated in combinatorial processing and the white matter tracts connecting them, the extent to which these regions are functionally specified for syntax, and if so, what their role is in the system remains an unsettled question, leaving much room for further investigation. In particular, specific syntactic deficits remain largely understudied, despite the insight they could provide both in terms of

conceptual as well as neurobiological models of syntax.

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