Neurolinguistics

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0   Introduction

Generative Grammar, from its inception, has been chiefly concerned with biolinguistics – the study of language as a characteristic psychological and biological trait of the human species (Berwick & Chomsky, 2016; Chomsky, 1965, 2000). This focus, with an accompanying "parts list" of computational mechanisms, enables scientists to investigate questions about the neurological implementation of language (Sprouse & Hornstein, 2016). However, there is much disagreement regarding which brain structures are involved in processing different aspects of language, and how linguistic computations are implemented neurobiologically. This chapter will give an overview of much of the research and recent developments on this topic, with a focus on the extent to which the Minimalist Program has influenced and potentially sharpened our understanding of the relation between language and brain. In principle, Minimalism facilitates the search for the neurobiological basis of linguistic mechanisms because it seeks to reduce the domain-specific component that must be uncovered in the brain to a minimum (Berwick et al., 2011). However, much of the research reviewed in this chapter has a somewhat unsatisfying localizationist character. As Jerry Fodor once said, "If the mind happens in space at all, it happens somewhere north of the neck. What exactly turns on knowing how far north?" (Fodor, 1999). Such *maps problems* (Poeppel, 2012) dominate research in cognitive neuroscience, and do not offer explanations of how the human brain gives rise to the language faculty. However, the aspiration espoused in this chapter is that addressing the maps problems may help the development of such explanations.

Section 1 introduces the currently dominant perspective regarding the syntax-brain relation: that Broca's area is the locus of core syntactic computations. It reviews the origins of this view from the study of agrammatic comprehension in aphasia in the 1970s. Section 1 will identify important issues with this line of research, stemming in large part from the difficulty of relating linguistic competence to actual language behavior or performance (Chomsky, 1965), a particularly pressing issue for neurolinguistics (for perspectives on this question, see Chapters 59 (Hunter) and 60 (parsing) of this handbook). Section 2 reviews the functional neuroimaging literature on syntax and how it relates to the dominant Broca's area-centric perspective. Researchers working from the perspective of functional neuroimaging often have failed to incorporate insights from modern aphasia research using lesion-symptom mapping into their conclusions about the neurological organization of syntax. Moreover, functional neuroimaging studies of syntax also suffer from competence-performance issues, although recent work has attempted to make explicit and test formal models of human sentence processing and correlate these with measures of brain activity (Brennan et al., 2016; Brennan & Pylkkänen, 2017; Nelson et al., 2017), which may help to move the field forward. Section 3 reviews recent work on syntactic *production* deficits in aphasia concerning an old but rarely studied distinction between agrammatism and paragrammatism. While agrammatism will likely be familiar to many readers, paragrammatism may not be. However, this syndrome may provide fertile ground

towards understanding the neurological organization of syntax. Section 4 introduces a recent model of syntax in the brain (Matchin & Hickok, 2020) that best accounts for both the functional neuroimaging and aphasia literatures. The model was inspired by the spirit of the Minimalist Program, particularly the proposed split between hierarchical and linear computation proposed by Chomsky, Berwick and colleagues (Berwick et al., 2013; Berwick & Chomsky, 2016; Chomsky, 2013, 2015). It was carefully developed to align with the appropriate level of linguistic granularity to line up with neuroanatomy, which results in a somewhat blurrier map of language in the brain than desired. Section 5 speculates about brain evolution and development inspired by this model.

1 The association between Broca's area and syntax

The work of Friederici and colleagues best represents the dominant viewpoint in the field regarding the localization of syntactic computation to Broca's area. Their main claim can be summarized by the following (Friederici, 2017a): "The data suggest that the basic syntactic computation of binding two elements into a phrase (called Merge) assumed by linguistic theory can be evidenced at the neurobiological level in a confined brain region, BA44 [the posterior part of Broca's area]". The model includes the additional provision that the posterior temporal cortex is the locus of the lexicon, resulting in a neat division of function between the two classic language areas of the brain (Figure 1). Several other authors have developed similar models positing the same basic division between Broca's area/syntax the temporal lobe/lexicon (Grodzinsky, 2000; Hagoort, 2005, 2014; Pinker & Ullman, 2002).
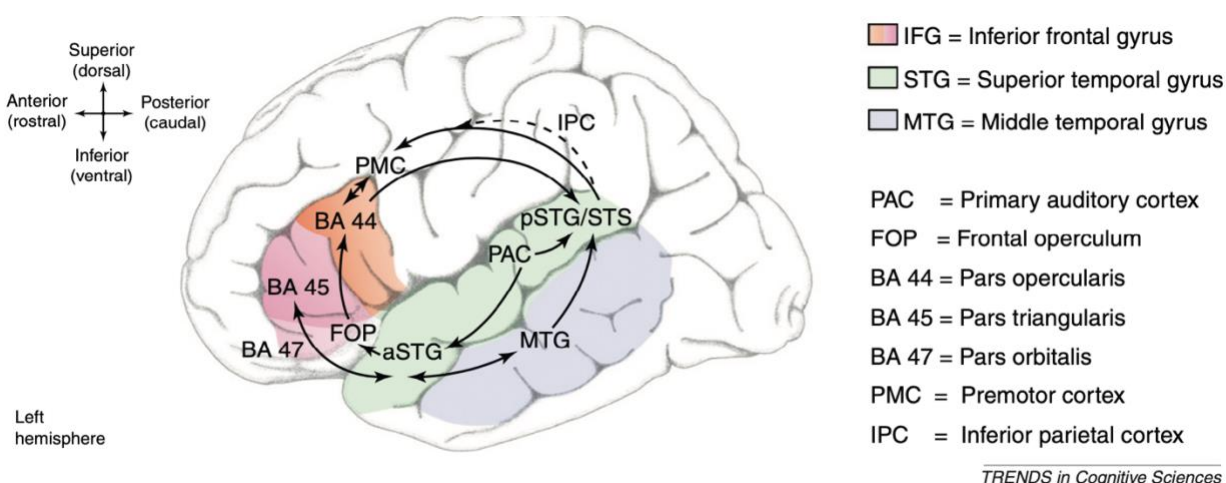
Figure 1 (figure and caption with permission from Friederici, 2012). The cortical language circuit (schematic view of the left hemisphere). The major gyri involved in language processing are colorcoded. In the frontal cortex, four language-related regions are labeled: three cytoarchitectonically defined Brodmann [39] areas (BA 47, 45, 44), the premotor cortex (PMC) and the ventrally located frontal operculum (FOP). In the temporal and parietal cortex the following regions are labeled: the primary auditory cortex (PAC), the anterior (a) and posterior (p) portions of the superior temporal gyrus (STG) and sulcus (STS), the middle temporal gyrus (MTG) and the inferior parietal cortex (IPC). The solid black lines schematically indicate the direct pathways between these regions. The broken black line indicates an indirect connection between the pSTG/STS and the PMC mediated by the IPC. The arrows indicate the assumed major direction of the information flow between these regions. During auditory sentence comprehension, information flow starts from PAC and proceeds from there to the anterior STG and via ventral connections to the frontal cortex. Back-projections from BA 45 to anterior STG and MTG via ventral connections are assumed to support top-down processes in the semantic domain, and the dorsal back-projection from BA 44 to posterior STG/STS to subserve top-down processes relevant for the assignment of grammatical relations. The dorsal pathway from PAC via pSTG/STS to the PMC is assumed to support auditory-to-motor mapping. Furthermore, within the temporal cortex, anterior and posterior regions are

connected via the inferior and middle longitudinal fasciculi, branches of which may allow information flow from and to the mid-MTG.

This general architecture has its origins in the work of aphasiologists, beginning in the early 1970s, regarding the nature of syntactic abilities of people with Broca's aphasia (for an in-depth review, see Matchin & Rogalsky, in press). Historically, aphasias have been classified with respect to various deficits in comprehension, production, and repetition (Damasio, 1992; Goodglass, 1993; Hillis, 2007), with little attention paid to linguistic theory (Lenneberg, 1973; Weigl & Bierwisch, 1970). Broca's aphasia is a well-known aphasia that is also one of the most common. The hallmark of Broca's aphasia is impaired, nonfluent production in the face of seemingly good comprehension and good awareness of deficits, associated with lesions to the frontal lobe (Goodglass, 1993). By contrast, Wernicke's aphasia is characterized by fluent (though disordered) production with poor comprehension and poor awareness of deficits, associated with posterior temporal-parietal lesions (Goodglass, 1993).

The production deficits in Broca's aphasia span many facets and are variable across individuals, including halting, effortful speech, phonetic and phonological speech disturbances, word finding issues, and *agrammatism*. Agrammatism is a "telegraphic" character of speech, with a tendency to omit function words, inflectional morphemes, and verbs, and an overall simplification of sentence structure (Goodglass, 1968). Below is an example of relatively severe agrammatic speech from Goodglass (1993):

> Yeah… Wednesday… Paul and dad… Hospital… yeah… doctors, two… an' teeth.

While some have suggested a non-syntactic explanation for agrammatic speech production (Kean, 1977, 1979; Kolk, 1995), it is fairly difficult to explain the full range of issues in expressive agrammatism without appeal to syntactic features or mechanisms of some kind (Matchin & Rogalsky, in press; see Fyndanis chapter, this volume).

Caramazza & Zurif (1976) questioned the assumption that people with Broca's aphasia have intact comprehension. They speculated that lexical and semantic aspects of comprehension might be preserved in these patients, but that they might have a central syntactic deficit underlying both sentence production and comprehension (Caramazza & Zurif, 1976; Schwartz et al., 1980; Zurif et al., 1972). This was sometimes called the "overarching agrammatism" hypothesis (Grodzinsky, 2000; Swinney & Zurif, 1995), with the additional claim that this central deficit resulted from damage to Broca's area. The seminal study by Caramazza & Zurif (1976) is widely cited as having clearly established this parallelism of syntactic deficits in both comprehension and production. However, there are serious challenges to this conclusion, as will be discussed after first reviewing the details of the study.

Caramazza and Zurif noted the classical dissociation between production abilities (impaired) and comprehension abilities (intact) in Broca's aphasia, yet questioned whether the seemingly intact comprehension abilities indicated an intact system of syntactic competence. A previous study from their group (Zurif et al., 1972) required Broca's aphasia patients to perform a metalinguistic task: sorting the words of sentences according to how they "went best together". A hierarchical clustering analysis of the data from control subjects resembled the phrase structure of the sentences (e.g. grouping a determiner with its noun complement). By contrast, the patients would group content words together and handled function words variably, all of which contradicted the groupings

dictated by phrase structure. In this light, Caramazza and Zurif pointed out that several researchers suggested that the relationship between grammatical theory to real-time language performance is likely to be indirect, with performance drawing upon additional mechanisms (Chomsky, 1965; Fodor et al., 1974; Miller & Chomsky, 1963). This raised the possibility that intact comprehension in Broca's aphasia might result from the use of intact heuristics such as surface-level word order regularities and semantic plausibility, but with impaired syntactic competence.

These observations motivated the experimental design of Caramazza & Zurif (1976): a manipulation of word order canonicity and semantic plausibility to test whether people with Broca's aphasia rely on these cues rather than a syntactic algorithm to interpret sentence meaning. The experiment contained four conditions: sentences with canonical word order and an animacy constraint, e.g. (1), sentences with non-canonical word order and an animacy constraint, e.g. (2), sentences with non-canonical word order without an animacy constraint, i.e., reversible, e.g. (3), sentences with non-canonical word order without an animacy constraint but had an implausible interpretation according to world knowledge, e.g. (4). They required subjects to point towards a picture that correctly resembled the meaning indicated by the sentence, and included a number of different foil types across trials; crucially, they included foils that depicted agent-patient role reversals between the noun phrases of the sentence, e.g., for (3), an image of a lion chasing the tiger.

1. Canonical, constrained: The boy is throwing a round ball.
2. Noncanonical, constrained: The apple that the boy is eating is red.
3. Noncanonical, reversible: The lion that the tiger is chasing is fat.
4. Noncanonical, implausible: The dog that the man is biting is black.

Focusing only on the trials including role-reversal foils (which test the thematic relations of the sentence), healthy control subjects performed at ceiling for most sentence types, except for the noncanonical, reversible sentences (example 3), for which they performed at about 90%. People with Wernicke's aphasia were impaired across the board, and importantly showed no effect of the semantic constraint or word order manipulation. People with Broca's aphasia were at ceiling for the canonical, constrained sentences, near ceiling for the noncanonical, constrained sentences, but at chance for both the noncanonical, reversible and noncanonical, implausible conditions. At the time, a fairly dominant view was that language comprehension only indirectly relied on grammatical mechanisms, and that comprehension was first accomplished via non-grammatical mechanisms and heuristics (Fodor et al., 1974). Caramazza & Zurif therefore accordingly reasoned that people with Broca's aphasia can comprehend sentences without appeal to grammatical representations, but failed when a grammatically-licensed syntactic parse was necessary. Thus, the authors suggested that people with Broca's aphasia have a central syntactic deficit underlying both their production and comprehension, i.e. the "overarching agrammatism" hypothesis. Combined with the assumption that people with Broca's aphasia consistently have damage to Broca's area, this line of research established a hierarchical syntactic function for this region.

The study of Caramazza & Zurif (1976) was highly influential. Not only did it strongly associate Broca's area with syntactic comprehension, it also led to the widespread adoption of reversible, complex, non-canonical sentence structures to assess syntactic abilities in aphasia. However, there is strong evidence that the comprehension of complex structures with non-canonical word order (such as English object-relatives) requires additional support relative to simpler, more canonical structures, particularly from working memory resources (Just & Carpenter, 1992; Rogalsky et al., 2008). Thus, work using these constructions likely conflates syntax with working memory. Importantly, in the

Caramazza & Zurif (1976) study, people with conduction aphasia, associated with speech repetition and phonological working memory deficits (Damasio, 1992), but mostly unimpaired sentence production and comprehension, showed the same profile of deficits as people with Broca's aphasia, likely due to the required working memory demands. This same explanation may in fact also apply to people with Broca's aphasia, who also tend to have working memory deficits (Caspari et al., 1998; Pettigrew & Hillis, 2014).

Further research supports the notion of intact syntactic processing in Broca's aphasia, and against the idea of a hierarchical syntactic function of Broca's area. In contrast to the standard paradigm of complex, non-canonical sentence comprehension, a simpler and more direct task to tap into syntactic competence is to ask subjects to rate the acceptability of grammatical and ungrammatical sentence structures. Studies of acceptability judgments in people with Broca's aphasia who showed selective difficulty in comprehension of sentences with noncanonical word order revealed largely intact acceptability judgment abilities in such patients when working memory demands are limited (Linebarger et al., 1983; Wilson & Saygın, 2004; Wulfeck, 1988). Additionally, the acute awareness of grammatical deficits and a general tendency to avoid making syntactic errors in Broca's aphasia patients suggests an intact syntactic system (Bastiaanse & van Zonneveld, 1998; Heeschen, 1985; Kolk & Heeschen, 1992). Finally, modern lesion-symptom mapping studies involving large groups of subjects with aphasia have strongly indicated that syntactic comprehension deficits are associated with temporal-parietal damage and not Broca's area damage (Dronkers et al., 2004; Kristinsson et al., 2020; Matchin et al., 2021; Matchin, Basilakos, et al., 2022; Pillay et al., 2017; Rogalsky et al., 2018; Wilson & Saygın, 2004). If Broca's area were the locus of basic syntactic mechanisms, whether described as Merge from the perspective of Minimalism or any other conceptualization, one would expect that lesions to this area should cause syntactic comprehension deficits, whether revealed through sentence comprehension or acceptability judgments. However, they do not. Thus the neuropsychological evidence, when reconsidering the interpretation of early findings, speaks strongly *against* the overarching agrammatism hypothesis, and against the concept of a hierarchical syntactic function of Broca's area.

An additional issue worth noting concerns the neuropathology of Broca's aphasia and expressive agrammatism. Several modern lesion-symptom mapping studies have supported the assumptions about the lesions involved in Broca's aphasia, finding associations between damage or degeneration of Broca's area and frontal cortex with agrammatic speech deficits or Broca's aphasia more generally (Den Ouden et al., 2019; Fridriksson et al., 2015; Matchin et al., 2020; Matchin, Basilakos, et al., 2022; Sapolsky et al., 2010; Wilson et al., 2010). However, Broca's aphasia patients without damage to Broca's area have been identified (Fridriksson et al., 2007), patients with damage restricted to Broca's area often do not have aphasia at all (Gajardo-Vidal et al., 2021; Mohr et al., 1978), and chronic Broca's aphasia reliably implicates damage to the posterior temporal lobe in addition to Broca's area (Fridriksson et al., 2015). These issues complicate some of the assumptions early studies made regarding the underlying lesions associated with Broca's aphasia, further loosening the selective link between damage to Broca's area and syntactic comprehension deficits. For example, it may be the case that not all the comprehension deficits observed in Broca's aphasia are due to working memory deficits, but rather syntactic deficits resulting from the rather large lesions extending into the posterior temporal lobe. Data from functional neuroimaging studies, reviewed below, help to inform these questions by providing insight into the organization of syntactic processing in the healthy brain.

2   Functional neuroimaging

The advent of non-invasive functional neuroimaging methods, such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and magnetoencephalography (MEG) in humans in the late 1980s and early 1990s led many researchers to turn their attention to experiments designed to localize syntactic mechanisms in the healthy brain. Such studies had many advantages over the study of aphasia, including the ability to look at intact rather than impaired processing (helping avoid functional reorganization in the brain and alternative processing strategies resulting impaired language). By now, studies using a large variety of methods, experimental manipulations, and languages (including sign languages) have localized syntactic comprehension abilities in the human brain (see Matchin, 2021 for a more comprehensive review). Most of these experiments have found similar patterns of activation in both Broca's area and the posterior temporal lobe, although some studies find activation primarily in one area or the other. These include various experimental manipulations: processing violations of word order, agreement, and verb subcategorization relative to grammatical sentences (Embick et al., 2000; Friederici, 2003; Husband et al., 2011; Kuperberg et al., 2000; M. Meyer et al., 2000; Moro et al., 2001; Rüschemeyer et al., 2005), processing of complex non-canonical structures relative to simpler and more canonical ones (Just et al., 1996; Stromswold et al., 1996), processing of fully structured phrases and sentences to less structured language or unstructured word lists (Fedorenko et al., 2012; Flick & Pylkkänen, 2020; Goucha & Friederici, 2015; Law & Pylkkänen, 2021; MacSweeney et al., 2006; Matar et al., 2021; Matchin et al., 2017; Matchin, Brodbeck, et al., 2019; Matchin, Liao, et al., 2019; Matchin, İlkbaşaran, et al., 2022; Mazoyer et al., 1993; Pallier et al., 2011; Zaccarella, Meyer, et al., 2017; Zaccarella & Friederici, 2015), and artificial grammar learning and processing (Bahlmann et al., 2008; Friederici et al., 2006; see Folia et al., 2010 for a review).

One type of experiment that is commonly used to identify a specifically syntactic function, as opposed to a conceptual-semantic one, is the use of *jabberwocky* (Carroll, 1871): sentences with the content words replaced by pseudowords but retaining function words and morphemes, e.g. *the tevill will sawl a pand* (Matchin et al., 2017). By contrasting such sentences with scrambled versions, increased activation presumably reflects mechanisms that are more specific to syntax rather than to the complex meanings typically associated with sentences. Such studies have in fact revealed that other areas sometimes associated with syntax, such as the anterior temporal lobe (J. Brennan et al., 2012; J. R. Brennan & Pylkkänen, 2017; Humphries et al., 2001, 2005, 2006), do not usually show jabberwocky structure effects, but routinely show activation in Broca's area and the posterior temporal lobe (Fedorenko et al., 2012; Goucha & Friederici, 2015; Matchin et al., 2017; Matchin & Wood, 2020; Pallier et al., 2011) (cf. Mazoyer et al., 1993 and Shain et al., 2021).

In general, posterior temporal activations during studies of syntactic processing are often dismissed as being associated with increased lexical activation during structure building (Snijders et al., 2009) or integration of syntax and semantics (Friederici, 2017b). This is in part because early functional neuroimaging research on semantic priming suggested a key role for posterior temporal cortex in early, automatic lexical access, with a role for frontal cortex in top-down controlled retrieval and selection of lexical items (see Lau et al., 2008 for a review). However, both regions show clear *lexicality effects*: increased activation for real words relative to pseudowords (Fedorenko et al., 2020; Goucha & Friederici, 2015; Matchin et al., 2017; Shain et al., 2021). On this point, Fedorenko et al. (2020) claimed that because brain areas claimed to be involved in syntax invariably show lexicality effects, we should reject linguistic theories that posit specialized syntactic mechanisms (e.g., all iterations of mainstream generative grammar) in favor of a holistic architecture in which both the linguistic form and meaning are integrated (such as construction grammar, e.g. Goldberg, 2003).

However, such a conclusion does not follow. First, mainstream generative grammar has posited a tight and inseparable relationship between the lexicon and syntax at least since Chomsky (1965). Second, and perhaps more critically, the relation between neurobiological phenomena and linguistic theory is fundamentally unclear (Embick & Poeppel, 2015; Poeppel & Embick, 2005), thus we should resist these kinds of reverse inferences (see also (Poldrack, 2006). The model of Matchin & Hickok (2020), reviewed in detail in Section 4, accounts for these phenomena by assuming that both Broca's area and the posterior temporal lobe instantiate integrated lexical-syntactic mechanisms, although with distinct representational properties.

Ultimately, there is no robust meaningful difference in activation patterns between these two regions with respect to syntactic processing (for an expanded review, see Matchin, 2021). This is supported by meta-analyses of neuroimaging studies of syntactic processing, which reveal that both of these areas are reliably implicated (Hagoort & Indefrey, 2014; L. Meyer & Friederici, 2016; Zaccarella, Schell, et al., 2017). Additionally, both regions show activation that is sentence-specific (Fedorenko et al., 2011); that is, these activations cannot be attributed to domain-general mechanisms that have been posited to account for language-related activations in Broca's area (Novick et al., 2005; Rogalsky et al., 2008; Rogalsky & Hickok, 2011; Thompson-Schill et al., 1997). Thus, it seems as though both Broca's area and the posterior temporal lobe are relevant to syntactic processing, at least broadly construed.

As reviewed in Section 2, there is far from compelling evidence that people with Broca's aphasia have syntactic comprehension deficits above and beyond other aphasia subtype. Critically, modern lesion-symptom mapping studies that systematically investigate the lesion correlates of syntactic comprehension deficits have associated these deficits primarily with posterior temporal, and not frontal, damage. Because of this, some authors have raised the possibility that syntax-related activations in Broca's area do not actually reflect syntactic mechanisms *per se*, but rather domain-general resources that are recruited to support linguistic processing, such as working memory, used to maintain information over time for processing or reanalysis, or cognitive control, which helps to resolve competition among competing parses (Hickok, 2000; Just et al., 1996; Kaan & Swaab, 2002; Novick et al., 2005; Rogalsky & Hickok, 2011; Thompson-Schill & Cutler, 2005). This is supported by the fact that the posterior subregion of Broca's area often thought to underlie syntax, BA44 or the pars opercularis, is commonly activated by phonological working memory and cognitive control tasks (Badre et al., 2005; Badre & Wagner, 2007; Braver et al., 1997; Buchsbaum et al., 2001; J. D. Cohen et al., 1997; Hickok et al., 2003; January et al., 2009; Rogalsky et al., 2008).

These proposals do not account for the fact that activation in the anterior part of Broca's area, the pars triangularis/BA45, cannot be attributed to domain-general mechanisms, as these areas do not activate in experiments designed to test such mechanisms (Fedorenko et al., 2011; Matchin et al., 2014; Rogalsky et al., 2008, 2015). This suggests a function of this region that is more specific to language. Matchin, (2018), consistent with previous proposals (Caplan & Waters, 1999; Fiebach et al., 2005; Rogalsky et al., 2015), put forward the hypothesis that this region supports syntactic working memory. This proposal should be distinguished from the idea that Broca's area instantiates a form of temporary store that supports syntactic computation, e.g. a pushdown stack (Fitch & Martins, 2014). Rather, it suggests that language-preferring subregions of Broca's area (i.e. pars triangularis/BA45) support an exceptional working memory system that is only needed to support particularly difficult processing circumstances, but is not necessary for basic structure building operations, although it may be regularly used to facilitate comprehension by predicting upcoming syntactic material (Bonhage et al., 2015; Jakuszeit et al., 2013; Matchin et al., 2017). The syntactic

working memory system proposed by Matchin (2018) is thought to be computationally isomorphic to the "phonological loop", relying on subvocal internal articulation to maintain information temporarily for further processing (Baddeley, 2003; Baddeley et al., 1981; Buchsbaum & D'Esposito, 2008), yet representationally-specific to lexical-syntactic representations.

While most functional neuroimaging studies indicate that both Broca's area and the posterior temporal lobe are both active during both comprehension and production of sentences (Menenti et al., 2011, 2012; Segaert et al., 2012, 2013), there are some data to suggest that the language-specific subregions of Broca's area are biased towards production, consistent with this rehearsal-based proposal of its function. Matchin & Wood (2020) performed an fMRI study in which subjects either comprehended long sequences of written text or performed a subvocal articulatory rehearsal task commonly used to study the phonological working memory loop (Buchsbaum et al., 2001; Hickok et al., 2003), but with structured phrases. This study showed that sentence-preferring subregions of Broca's area and the posterior temporal localized in individual subjects showed an asymmetry of activation with respect to comprehension and the rehearsal task: the posterior temporal lobe was activated more by syntactic comprehension than syntactic production, whereas Broca's area was activated relatively equally by both. These results suggest a relative bias in the syntax-related function of Broca's area towards production when compared to the posterior temporal lobe, which would be consistent with a role focused on internal articulation rather than basic syntactic computations. This possibility is explored more deeply in Section 4, which reviews the novel neurobiological architecture for syntax proposed by (Matchin & Hickok, 2020).

All of the studies discussed above, conforming to the dominant experimental paradigm for most of the history of functional neuroimaging studies, rely on artificial experimental designs that manipulate the psychological variables of interest. However, an approach that has recently gained traction is to use "naturalistic" approaches, i.e. the use of more complex, uncontrolled materials (e.g. an audiobook) and including statistical regressors for a variety of variables of interest (e.g. the time of presentation for each word) as well as nuisance, confounding variables (e.g., the amplitude of the stimulus at each time point) (J. Brennan, 2016; Huth et al., 2016; Sonkusare et al., 2019). These approaches, coupled with psychologically-plausible parsing models that obey the grammatical constraints specified in syntactic theory (Hale, 2014), can in principle narrow down the brain regions of interest for syntactic processing in a much more precise way than standard approaches. These studies have so far associated very similar brain regions with syntactic parsing operations, i.e. (mostly) left-lateralized perisylvian regions including Broca's area and the posterior temporal lobe (Bhattasali et al., 2019; J. R. Brennan et al., 2016; J. R. Brennan & Pylkkänen, 2017; Nelson et al., 2017; Shain et al., 2020). However, the potential fruit of this approach is that it makes much more explicit the relationship between the syntactic mechanisms and constraints posited in linguistic theory and the brain signals generated in functional neuroimaging studies. In particular, these studies claim that the observed signals reflect domain-general cognitive processing architectures that have been specialized for syntax that allow structure to be processed in real-time. In the future, this may facilitate the development of more specific hypotheses about the brain substrates of the central syntactic mechanisms and the processing systems these relate to.

3   Distinct syntactic production deficits in aphasia: agrammatism and paragrammatism

There is only minimal evidence so far from functional neuroimaging studies to suggest a meaningful distinction in function between Broca's area and the posterior temporal lobe with respect to production and comprehension. This distinction is best exemplified with respect to the lesion-

symptom mapping data in people with aphasia. We reviewed above how agrammatic production deficits are strongly associated with damage to the frontal lobe, including Broca's area, and syntactic comprehension deficits are strongly associated with damage to the posterior temporal lobe, and not vice versa. The dichotomy between production-oriented linguistic systems in the frontal lobe and comprehension-oriented linguistic systems in the temporal lobe aligns with the early model of Wernicke (Wernicke, 1874), who proposed such a dichotomy without specifying the linguistic detail. However, it would be unsatisfying to end the story there, with the conclusion that the brain systems that support syntactic processing in production and comprehension are totally distinct. Linguistic theory has driven home the concept of central linguistic systems that are accessed for both production and comprehension, or even used for spontaneous thought without overt communication (Chomsky, 2000). Thus, if the posterior temporal lobe in fact processes the central systems of hierarchical structure, we would expect that damage to this region produces deficits in both comprehension *and* production.

While it is certainly the case that agrammatic production is primarily associated with frontal damage, a different sort of syntactic production deficit in aphasia is in fact associated with posterior temporal damage: *paragrammatism*. Kleist (1914) postulated that there are fundamentally two kinds of syntactic deficits in sentence production: agrammatism, the omission of function words and morphemes and overall simplification of grammatical structure, and paragrammatism, the misuse of grammatical elements and structures. Some examples of paragrammatic speech in English are illustrated below, with the ungrammatical section marked in bold:

> "Anyway we had **a birds** coming out of our ear" (Yagata et al., 2017)
> "He **had build** a h- h- home for the birds" (Yagata et al., 2017)
> "And I want everything to be **so talk**" (Butterworth & Howard, 1987)
> "She **was handled to look** at the books a bit" (Butterworth & Howard, 1987)
> "I'm **very want** it" (Butterworth & Howard, 1987)
> "**Isn't look** very dear, is it?" (Butterworth & Howard, 1987)
> "But **it's** silly, **aren't they**?" (Butterworth & Howard, 1987)

While much work has focused on agrammatism, likely due to its striking, obvious character and association with damage to Broca's area, there has been much less work probing the character and lesion correlates of paragrammatism. Some authors have claimed that there is no meaningful functional distinction between agrammatism and paragrammatism, and that both disorders stem from the same underlying grammatical deficit, with the agrammatism/paragrammatism distinction merely an artifact of speech fluency and the willingness to produce overt grammatical errors (Heeschen, 1985; Heeschen & Kolk, 1988; Kolk & Heeschen, 1992). However, other authors have noted qualitative differences in the grammatical deficits in the speech of agrammatic and paragrammatic patients (Goodglass et al., 1993).

A true underlying distinction between agrammatism and paragrammatism is supported by the distinct neuropathological bases of these syndromes. Paragrammatism is strongly associated with the fluent aphasias, including Wernicke's and conduction aphasia (Goodglass et al., 1993), which are associated with posterior temporal-parietal lesions (Buchsbaum et al., 2011; Ogar et al., 2011). Case studies have also shown an association between posterior temporal damage and paragrammatic speech (Yagata et al., 2017). A recent performed a large-scale lesion-symptom mapping analysis of agrammatism and paragrammatism in order to confirm that the lesion correlates of paragrammatism itself are in fact localized to posterior temporal cortex (Matchin et al., 2020). In a group of 53 people

with aphasia and left hemisphere lesions, each subject's speech was classified as agrammatic, paragrammatic, or no grammatical deficit (or both agrammatic and paragrammatic). The analyses revealed a clear double dissociation: agrammatism is associated with frontal damage, including Broca's area, and not posterior temporal damage, while paragrammatism is associated with posterior temporal-parietal damage and not frontal damage (Figure 2). This distinction holds even when accounting for the overall differences in speech rate, which indicates that the distinction between these syndromes is not merely an artifact of fluency/acceptance of overt errors and suggests that there are in fact two qualitatively distinct forms of syntactic speech production deficits in aphasia.
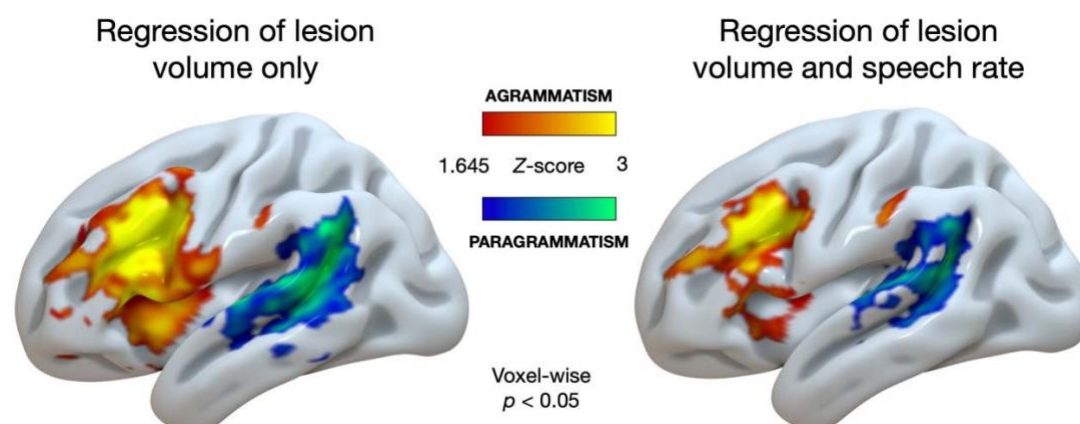

Figure 2 (figure and caption from Matchin et al., 2020 under the CC BY 4.0 license). Uncorrected whole-brain analyses (voxel-wise p < 0.05) of the effects of AGRAMMATISM (red-yellow) and PARAGRAMMATISM (blue-green) displayed on the cortical surface an inflated left- hemisphere brain template in MNI space. Left: only lesion volume included as a covariate. Right: both lesion volume and speech rate (words per minute) included as covariates. AGRAMMATISM = effect of agrammatism (AGRAMMATIC, including BOTH > NO GRAMMATICAL DEFICIT and PARAGRAMMATIC, excluding BOTH), PARAGRAMMATISM = effect of paragrammatism (PARAGRAMMATIC, including BOTH > NO GRAMMATICAL DEFICIT and AGRAMMATIC, excluding BOTH).

With only relatively preliminary investigations into the syntactic deficits identified in paragrammatism, it is hard to make completely firm conclusions regarding the specific deficits in underlying linguistic functions. Matchin et al. (2020) suggest that paragrammatic patients are able to generate fluent sequences of words and morphemes relying on intact frontal production-related systems, but are unable to constrain their utterances with hierarchical representations, leading to errors. Consider one common type of paragrammatic error: agreement mismatch. Agreement relies on a local hierarchical computation, with the agreeing elements potentially linearly far apart (Chomsky, 2001). It follows that a hierarchical deficit could lead to in inability to perform the agreement computation, leading to potential errors. In general, patients with paragrammatism (and posterior temporal damage) generate speech without much awareness of the ill-formedness of their utterances, which coincides with the fact that posterior temporal damage is associated with acceptability judgment deficits (Wilson & Saygin, 2004). In other words, it seems as though patients with posterior temporal damage are unaware of syntactic ill-formedness of others' language as well as their own.

In stark contrast, patients with agrammatic production (and inferior frontal damage) hesitate to produce inflected forms or complex sentences at all. However, their production is not erroneous. In fact, they are quite sensitive to the deficient nature of their utterances and seem to avoid making errors (Bastiaanse & van Zonneveld, 1998). This suggests intact knowledge of hierarchical syntactic structure. Rather, their deficits can be more straightforwardly explained by appealing to deficits

downstream from hierarchical syntactic computation. This lines up well with the fact that agrammatic patients generally perform well on acceptability judgment tasks (Linebarger et al., 1983; Wulfeck, 1988) and sentence comprehension tasks (Rogalsky et al., 2018), and that damage to Broca's area does not produce notable deficits in acceptability judgments relative to other lesion locations (Wilson & Saygın, 2004). The comprehension deficits that can be observed in agrammatic patients, e.g., for reversible object-relative sentences, which are thought to require increased working memory resources, are straightforwardly explained by working memory deficits in these patients (Hickok, 2000; Matchin & Rogalsky, in press; Pettigrew & Hillis, 2014). Section 4 reviews the model of Matchin & Hickok (2020), which posits that the role of sentence-selective subregions of Broca's area are not to perform hierarchical syntactic computations, but rather to produce linearized morpho-syntactic sequences for speech output (for related proposals, see Boeckx et al., 2014; Bornkessel et al., 2005), and that a deficit in this ability explains the classic syndrome of expressive agrammatism.

4   A Minimalism Program for neurolinguistics: starting at the interfaces

Linguistics and neuroscience have distinct, and possibly incommensurate, ontologies (Embick & Poeppel, 2015; Poeppel & Embick, 2005). For example, does Merge correspond to a sizable chunk of brain tissue, containing tens of thousands of neurons, acting in concert as a connectionist neural network? Or does it exist at a much subtler level of brain organization, such as the structure of synaptic connections, biochemical processes, or neural oscillations? As of now there is no clear answer, as with the question of how many basic aspects of cognition are implemented neurobiologically (Gallistel & King, 2010). The push to "localize Merge" in some experiments results from a misguided desire to align the "parts list" of language directly to large chunks of brain tissue (as discussed in Section 2, progress on explicitly relating competence to performance via computational models will be essential to help resolving this issue).

However, the alternative in developing useful neurobiological models of language in the brain is far from clear, as it is hard to determine what functional labels to assign to different components (e.g., brain regions) of the model. The model of Matchin & Hickok (2020) reviewed below assumes it is appropriate to broadly associate different regions of the brain with different representational contents, namely hierarchical vs. linear syntactic relations. Note that the model does not suggest that we can do away with Merge, as is suggested by some authors (Christiansen & Chater, 2008; Goldberg, 2003, 2004; Tomasello, 2009). Rather, a simple syntactic operation like Merge probably does not correspond to a specific brain area, but rather may be implemented by a much subtler property of brain organization, such as the connectivity dynamics within the posterior temporal lobe, or cortical-subcortical oscillatory mechanisms (Murphy, 2015; Murphy et al., 2022).

One question we may be able to answer with somewhat greater confidence is whether the move from earlier instantiations of generative grammar, such as Government and Binding (Chomsky, 1981), to Minimalism has facilitated the development of neurobiological frameworks for language. Certainly this theoretical transition has resulted in changes to neurolinguistics. For example, the focus in Minimalism on a single layer of hierarchical structure generated by recursive Merge has led to an increased focus on constituency in neurolinguistics as a core problem to address (Ding et al., 2016; Matchin, Brodbeck, et al., 2019; Matchin, İlkbaşaran, et al., 2022; Nelson et al., 2017; Pallier et al., 2011; Zaccarella, Meyer, et al., 2017; Zaccarella & Friederici, 2015). But does the Minimalist Program have any *unique* purchase on our understanding of language in the brain relative to other linguistic approaches? Probably not, as all models of linguistic theory incorporate hierarchical

structure. However, as reviewed in this section, the model of Matchin & Hickok (2020) was inspired by the Minimalist hypothesis of Berwick & Chomsky (2016) in separating out the computational mechanisms of hierarchy and linear order, associating the latter with much evolutionary older and conserved capacities, and the former as a novel and potentially human-unique computation. The success of the Matchin & Hickok model suggests that there has been at least some purchase gained by Minimalist speculation, in its spirit if not necessarily in terms of detailed theoretical postulates. An overview of this model is reviewed below.

The innovation of Minimalism relative to previous incarnations of Generative Grammar is not Merge, despite the prominent mention of this mechanism in the literature. In the words of Chomsky (2005): "Either Merge or some equivalent is a minimal requirement" because "an elementary fact about the language faculty is that it is a system of discrete infinity". Rather, the key insight is the possibility of reducing to a bare minimum the complex innate, language-specific machinery beyond Merge that seems necessary for effectively constraining language acquisition. This is accomplished in part by speculating about the computational demands of the systems that a language must interface with: those for conceptual-intensional (CI) interpretation and sensory-motor (SM) externalization.

Chomsky, Berwick and colleagues (Berwick et al., 2013; Berwick & Chomsky, 2016; Everaert et al., 2015) have emphasized that these two interfaces have fundamentally distinct roles in language. Hierarchical structure feeds semantic interpretation at the CI interface (Everaert et al., 2015; Heim & Kratzer, 1998), augmenting "a conceptual system for inference, interpretation, planning, and the organization of action – what is informally called 'thought' " (Berwick & Chomsky, 2016). Linear relations by contrast do not relate to semantics but rather appear to be imposed by demands of externalization – that is, in expressing language through the vocal tract (or, for sign language, the hands, head, and torso; Sandler & Lillo-Martin, 2006). Idsardi & Raimy (2013) have proposed that hierarchical structure is linearized in discrete stages, each adding incrementally more detailed linear relations until the representation is suitable for phonetic expression. Under this proposal, initial stages of linearization correspond to the linear components of morpho-syntax, that is how phrases, words and morphemes are ordered, while later stages of linearization provide increasing phonological detail, down to the level of segments. In Chomsky's (1995) approach, much of language acquisition consists in acquiring idiosyncratic aspects of language (i.e. the lexicon) rather than procedures for building hierarchical structures themselves. According to Berwick et al. (2013) and Berwick & Chomsky (2016), these idiosyncratic aspects prominently include the retuning of domain-general linearization procedures for the externalization of hierarchical structure.

While it is unclear how cognitive processes are implemented in the brain in computationally explicit detail, there are highly reliable mappings between different types of representation and brain areas. The distinction between primary and secondary sensory-motor cortex and association cortex has been well-established for a long time. Sensory and motor cortex (i.e. core aspects of SM) are densely interconnected with the peripheral nervous system, while association cortex, thought to underlie more abstract processes, lies in-between sensory-motor cortices. A meta-analysis and review by Binder and colleagues (Binder et al., 2009) has suggested that an internal capacity "…to use language productively, plan the future, solve problems, and create cultural and technological artifacts", that is, roughly what we might think of as the CI interface, is localized to a large-scale network of association cortex. This same network has been repeatedly identified in many studies of conceptual-semantic processing since then (Hodgson et al., 2021), and it overlaps with the so-called "default mode network" (Binder, 2012), that is, brain regions that are more active during rest periods than during sensory-motor processing, which likely reflects spontaneous thought or "mind-wandering".

We can use our understanding of the neurobiology of these aspects of SM and CI to inform us about where syntax might be localized in the brain, as the functional organization of the brain is likely driven in part by minimal connectivity distance between functionally-associated regions (Cherniak, 1994; Chklovskii et al., 2002; Chklovskii & Koulakov, 2004). This suggests that a brain area for hierarchical syntactic computation could be ideally located adjacent to the CI interface, given the apparent primary role for hierarchy in semantic interpretation, and a brain area for morpho-syntactic linearization could be ideally located adjacent to the SM interface, given the necessity of linear order for externalization. This is a key motivation for the model of syntax in the brain of Matchin & Hickok (2020) shown in Figure 3. The model is based on the dual-stream architecture previously proposed for speech processing that did not adequately incorporate syntax (Hickok & Poeppel, 2000, 2004, 2007). This dual-stream architecture proposes that a ventral stream is essential for the processing of meaning, whereas a dorsal stream is essential for transformation of a linguistic representation to a sequence of motor commands.
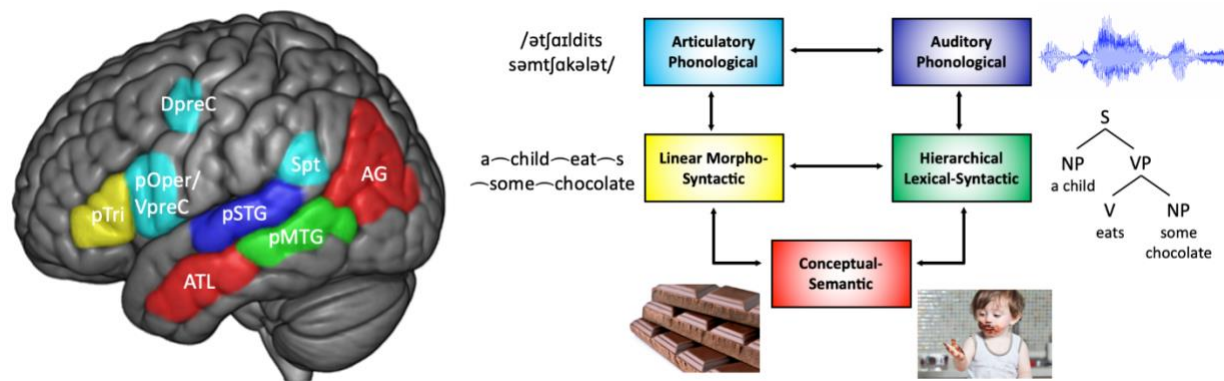

Figure 3 (figure and caption from Matchin & Hickok, 2020). Cortical organization of syntax and the sensorimotor and conceptual-semantic brain systems it interfaces with. pOper/VpreC, inferior frontal gyrus, pars opercularis/ventral precentral gyrus; DpreC, dorsal precentral gyrus; pSTG, posterior superior temporal gyrus (including dorsal bank of STS); pMTG, posterior middle temporal gyrus (including ventral bank of STS). Colored boxes correspond to the same colored brain regions. Arrows indicate bidirectional white matter connections between brain regions.

Red areas denote key regions in CI, though do not exhaust the cortical territory associated with this interface, as reviewed above. Damage to these areas is implicated in language comprehension deficits (Hickok & Poeppel, 2004). Blue areas denote SM – dark blue, perceptual; light blue, motor. These systems occupy secondary auditory and motor cortex - processing sound and speech at more abstract levels than primary auditory and motor cortex. For instance, damage to light blue regions causes phonological deficits in aphasia and apraxia of speech (Basilakos et al., 2015; Stark et al., 2019), whereas damage to the dark blue posterior superior temporal gyrus (pSTG) region causes speech perception deficits (Fridriksson et al., 2018; Hillis et al., 2018). Recent electrocorticography studies, with exquisite temporal and spatial resolution, have shown that the pSTG is involved in transforming a phonetic representation into a phonological one (Chang et al., 2010; Fox et al., 2020; Mesgarani et al., 2014; Sjerps et al., 2019; Tang et al., 2017). While there are plenty of open questions and debate regarding the functional organization of these systems, the general picture presented here is supported by strong empirical evidence.

A priori, given the assumption of optimal connectivity minimization (Cherniak, 1994; Chklovskii et al., 2002; Chklovskii & Koulakov, 2004), we expect a brain region responsible for hierarchical lexical-syntactic representations to be localized adjacent to the CI interface, and a brain region responsible for processing linear morpho-syntactic representations to be adjacent to the production-related parts of the SM interface. This is because the model assumes that the linear order of the stimulus does not need to be explicitly computed for comprehension (Lewis et al., 2006; Lewis & Vasishth, 2005), but must be computed in order for language to be overtly produced. Accordingly, Figure 3 shows the hierarchical lexical-syntactic system in green, the posterior middle temporal gyrus (part of the posterior temporal lobe, pMTG), directly embedded in the CI interface regions in red, and the linear morpho-syntactic system in yellow, the inferior frontal gyrus pars triangularis (pTri), just anterior to the articulatory phonological system. Both systems are posited to be lexicalized, that is to process syntactic information that is tied to individual lexical items as well as abstract stored pieces of structure.

Note that the pMTG syntactic system is adjacent to the 'S' part of the SM interface (pSTG, dark blue), well-positioned to support language comprehension by receiving phonological inputs from the periphery (analogously, we assume that sign language comprehension involves perceptual processing in posterior occipital-parietal cortex specialized for motion, space and form, also located near the pMTG). Not depicted in Figure 3 is the well-known white matter tract, the arcuate fasciculus, which connects the pMTG to the frontal lobe, including pTri (Catani et al., 2005; Yagmurlu et al., 2016). According to this proposal, the arcuate allows for the hierarchical-linear conversion, with linearization processes at the highest level in the pTri, lower levels of linearization more posteriorly into the articulatory phonological system, with primary motor cortex allowing for detailed phonetic instantiation (see Boeckx et al., 2014 and Bornkessel et al., 2005 for related linearaization proposals involving frontal areas, and Bornkessel-Schlesewsky & Schlesewsky, 2013 for a sequence-based dorsal processing stream).

What causes the routinely observed syntax-related activation in Broca's area during sentence comprehension? Matchin & Hickok (2020) suggest that this reflects the use of language-specific working memory resources for prediction of upcoming elements and to reiterate the sequence of perceived morphemes if structural revision is required (Fiebach et al., 2005; Matchin, 2018; Matchin & Rogalsky, in press; Rogalsky et al., 2015). These resources may be particularly valuable in difficult processing environments, particularly for difficult structures such as those with noncanonical word order or multiple embeddings, but are not strictly necessary for parsing the basic syntax of a sentence, given that hierarchical parsing relevant for comprehension may occur without explicit computation of linear order (Lewis et al., 2006; Lewis & Vasishth, 2005).

In contrast to most extant models of syntax and the brain (Friederici, 2017a; Hagoort, 2005; Pinker & Ullman, 2002) this model does not posit distinct localization for syntax and the lexicon. Rather, it proposes that the lexicon itself, previously thought to be localized to the pMTG, is also the locus of syntactic representations. This follows from a several considerations. First, empirically, lexical-semantic manipulations and syntactic manipulations typically overlap in the brain (Fedorenko et al., 2012; Matchin, Brodbeck, et al., 2019; Matchin et al., 2017). This is supported by the fact that people with fluent aphasia tend to have lexical-semantic deficits in their speech output in addition to paragrammatism (Butterworth & Howard, 1987). Second, all syntactic theories promote some degree of "lexicalization" of syntactic structure, that is bits of structure stored along with words. Finally, under a bare phrase structure approach (Chomsky, 1995), the labels of groups formed from applications of Merge are derived from underlying lexical elements instead. All of these observations

point to a tight relationship between the lexicon and structure, and that at least some aspects of syntactic structure are lexicalized – this makes the localization of the lexicon and syntax to the same brain area plausible.

This model does not solve the hardest problems of relating linguistic theory to the brain – that is, identifying how the brain actually implements linguistic computations. However, it does represent real progress over the stubbornly dominant perspective of the last few decades that Broca's area is the locus of the syntactic computations posited in generative grammar, which has changed only terminologically by calling this region the locus of Merge. While the Minimalist Program has not been decisive in detail in changing our understanding of the neurobiology of language, the proposal to fundamentally separate out the linear aspects of syntactic computation from the hierarchical ones that feed semantic interpretation has been fruitful in making sense of the neuroanatomical organization in its broad strokes. The next section is more speculative, using the Matchin & Hickok model as the basis for hypotheses into the evolution of the human language capacity and how it develops in the brain according to broad tenets of Minimalism.

5   Development and evolution

As discussed above, a key aspect of the Minimalist Program is assessing the extent to which language acquisition can be understood as harnessing and retooling domain-general mechanisms externalize the hierarchical structures generated by the basic property of language, i.e. Merge and the abstract lexical atoms, which seemingly emerged relatively late and suddenly in the hominin lineage (Berwick et al., 2013; Berwick & Chomsky, 2016; Bolhuis et al., 2014; Chomsky, 2005; Tattersall, 2019). How do these Minimalist assumptions regarding the emergence and development of the language faculty line up with the current state of neurobiological research? According to this approach, we would expect that the brains of humans differ from nonhuman primates in at least two relevant ways. First, we can expect whatever property of the brain corresponds to the "slight rewiring" that led to the emergence of the language faculty to be present in humans at a very early age, at least as early as infants have been demonstrated to represent hierarchical syntactic relations, which according to recent reports may be as early as 1.5 years (Lidz et al., 2017; Perkins & Lidz, 2021). Second, there may be major changes in brain organization that occur over a longer period of linguistic development, reflecting the harnessing and retooling of innate but domain-general sequencing systems into specialized subsystems that externalize language. This follows from the fact that humans continue to learn linguistic constructions, and in fact, whole languages, throughout the lifespan, and the fact that the development of sentence production generally lags significantly (in both qualitative and quantitative ways) behind comprehension (Clark & Hecht, 1983). The following section briefly reviews and speculate on research concerning these two neurobiological properties that have two distinct timescales of emergence.

The brains of humans and nonhuman primates such as chimpanzees and macaque monkeys differ in a variety of ways, most obvious of which is size: human brains are larger (Kaas, 2008). The association cortex, involved in the aspects of cognition most removed from primary sensory and motor abilities, is particularly expanded in humans relative to macaque monkeys (Hill et al., 2010). This suggests that later hominin evolution involved important changes to complex, abstract cognitive abilities, including language. Many researchers have sought to tie more specific properties of brain morphology in humans to the emergence of the language faculty. Perhaps the most celebrated of these is the observation that the planum temporale, a region adjacent to primary cortex in the vicinity of classic Wernicke's area, is larger in humans in the left hemisphere than the right in

about two of every three people (Geschwind & Levitsky, 1968; for a review see Shapleske et al., 1999). The pertinence of this anatomical observation to the evolution of the language faculty consists of two key facts: first, the planum temporale roughly corresponds to one of the classical language areas of the brain, and second, in most individuals, language is lateralized to the left hemisphere (Damasio, 1992; Geschwind, 1970; Springer et al., 1999; Wilson, Yen, et al., 2018), although this lateralization is modulated somewhat by handedness (Ocklenburg et al., 2014), or perhaps more accurately, genetic predisposition to handedness (Hancock & Bever, 2013).

However, subsequent research casts doubt on the plausibility of a leftward asymmetry of the planum temporale as the "slight rewiring" of the brain that supported the emergence of language. First, a similar proportion of left-right asymmetries in the size of the planum temporale has been observed in chimpanzees (Gannon et al., 1998), also modulated by handedness (Hopkins & Nir, 2010). This strongly speaks against this lateralization as a human-unique property of brain organization. In addition, the planum temporale has been strongly linked to higher-level auditory processing and motor control abilities (Hickok & Saberi, 2012), and not the syntactic and semantic functions characteristic of human language that underlies spoken, written, and sign language, located more inferiorly in the middle-posterior superior temporal sulcus (part of the posterior temporal lobe) (Matchin, İlkbaşaran, et al., 2022; Wilson, Bautista, et al., 2018). In fact, recent lesion-symptom mapping research in aphasia has associated the classical deficits of Wernicke's aphasia with damage not to the planum temporale but rather to the middle superior temporal gyrus and middle-posterior superior temporal sulcus (Matchin et al., 2021), suggesting that Wernicke's area, defined functionally, is not actually located in the planum temporale.

While there is substantial evidence against the hypothesized link between the left-right asymmetry of the planum temporale and the emergence of the human language faculty, the logic of this hypothesis can be preserved when further examining the anatomy of the posterior temporal lobe. In studies reported by Glasel et al., (2011) and Leroy et al. (2015), the sulcus or groove underlying the middle-posterior temporal lobe (straddling the brain regions identified in Figure 3 for lexical-syntactic processing green, and conceptual-semantic interpretation, red) was shallower in the left hemisphere than the right in all 14 human infants studied, a brain feature described as the "superior temporal asymmetrical pit", or STAP (Figure 4). Furthermore, this left-right asymmetry of the STAP did not change across the lifespan and was absent in chimpanzees (Leroy et al., 2015). It is not clear exactly what the increased shallowness of the left superior temporal sulcus reflects. One possibility is that it reflects increased density of white matter connections in this region, as this region is known to have uniquely great connectivity with brain regions associated with conceptual-semantic processing (Turken & Dronkers, 2011). Regardless, this anatomical feature is spatially located very close to the posterior temporal lobe brain area identified for lexical-syntactic processing across the studies reviewed in this chapter. Given its presence at least as early as hierarchical syntactic competence can be demonstrated (Lidz et al., 2017; Perkins & Lidz, 2021) it is a strong candidate to reflect the minimal neurobiological change that may have occurred in humans underlying the emergence of language.
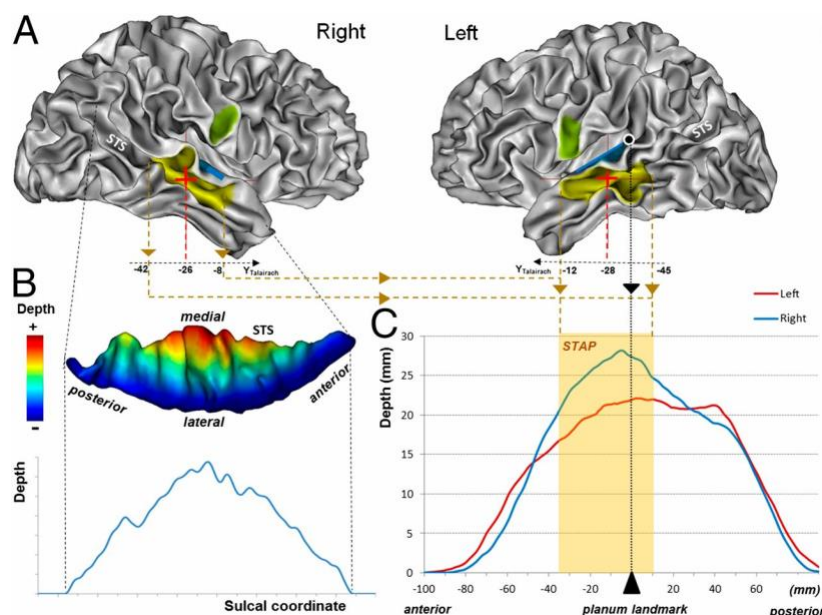
Figure 4 (figure and caption from Leroy et al., 2015). (A) Location of the STAP (yellow) relative to Heschl's gyrus (blue) and the ventral tip of the central sulcus (green) on both left and right inner cortical surfaces of an individual adult brain. The STAP center is shown by a cross. The black dot with a white contour line shows the planum temporale landmark. (B, Upper) Sulcal depth shown by color coding of the sulcal mesh (seen from above). (Lower) Sulcal depth profile in the right hemisphere of an individual subject. (C) Adult sulcal depth profile; STAP anterior and posterior ends as well as the planum landmark are drawn in dotted lines. The light orange overlay illustrates the STAP (deeper on the right), defined as the common asymmetrical segment in the three typical groups (infant, right- handed children, and adults).

Another anatomical feature of the human brain highly relevant for language that distinguishes it from non-human primates is the white matter tract connecting the posterior temporal lobe to Broca's area, the arcuate fasciculus (Geschwind, 1979). This tract has been shown to be less robust in non-human primates, with greatly expanded temporal lobe connectivity in humans (Rilling et al., 2008). Friederici, Berwick, and Chomsky (Berwick & Chomsky, 2016; Friederici, 2017a; Friederici et al., 2017) discuss this tract as an alternative hypothesis regarding a minimal change to brain organization that may have led to the emergence of hierarchical syntactic abilities in humans. This view is predicated on the assumption that a subregion of Broca's area, BA44, instantiates basic syntactic computations. They note that the speed and accuracy with which subjects process complex non-canonical sentences (object-extracted relative clauses) correlates with the development of the arcuate fasciculus (Skeide et al., 2016), and that it is not fully developed in children (Dubois et al., 2006, 2008; Perani et al., 2011). There is also evidence to suggest that the emergence of the full connectivity of this tract relies on exposure to linguistic data in childhood and is correlated with first language competence: people born deaf to hearing parents who were not exposed to sign language until adolescence appear to have a selectively less developed left hemisphere arcuate fasciculus (relative to other white matter tracts) compared to deaf native signers of American Sign Language (Cheng et al., 2019). Overall, Friederici and colleagues suggest that the increased strength of this tract over a long period of development increasingly allows for the syntactic computations in Broca's area to be integrated with semantic information in the temporal lobe (Friederici et al., 2017).

However, the long timescale under which the development of the arcuate fasciculus occurs (into adolescence), and the "syntactic" abilities that correlate with its development (comprehension of complex non-canonical sentences), casts doubt that it reflects the minimal evolutionary brain change in humans that led to the emergence of the language faculty. First, we would expect that this feature

of the brain would *support* the acquisition of language, present early on. Another way of saying this is that even the brains of humans who do not learn language should contain this property of the brain, because they could have. The fact that the strength of the arcuate is contingent on exposure to language data and emerges only quite late in development (well past the earliest stages that hierarchical syntactic competence can be demonstrated) suggests that this feature reflects learned, not innate, properties of language. Second, the complex "syntactic" abilities that correlate with the development of the arcuate (comprehension of object-relative structures) are well known to require cognitive resources beyond phrase structure composition, such as working memory and attention (Gibson, 1998; Just & Carpenter, 1992; King & Just, 1991; Lewis et al., 2006; Miller & Chomsky, 1963; Novick et al., 2005). These are the very mechanisms thought to be supported by frontal cortex by many authors, as reviewed in Sections 1 and 2.

Thus, we can speculate that the unique strength and connectivity of the arcuate fasciculus in humans actually reflects the second important human-specific brain property discussed at the beginning of this section: the specialization of linearization procedures for externalization of language. Matchin (2018) suggested that we can understand this as a form of *neuronal retuning*, by which innate, domain-general computational mechanisms can be adapted for linguistic representations. The retuning framework is inspired by the work of Dehaene, Cohen and colleagues, which has been applied to a number of domains, but particularly with respect to reading (L. Cohen et al., 2000; Dehaene et al., 2015; Dehaene & Cohen, 2007, 2011). They explain the presence of brain areas specialized through reading through the harnessing of domain-general properties of high-level visual cortex, specializing them for orthographic forms through interaction with brain areas specialized for language. Applying this framework to language acquisition, we would expect subregions of prefrontal cortex to acquire a language-specific character; that is, they would become specialized for linguistic externalization through interaction with brain areas involved in processing hierarchical syntax (Matchin, 2018). With respect to the model of Matchin & Hickok (2020), we can speculate that subregions of Broca's area are gradually harnessed to become specialized for different aspects of linguistic linearization through interaction with the posterior temporal lexical-syntactic posterior temporal region, mediated through the arcuate fasciculus.

6   Conclusions

The neurobiological framework developed in Section 3, was inspired by Minimalist theorizing regarding the distinction between hierarchy and linear order in syntax. Furthermore, the speculation in Section 4 was guided by the Minimalist drive to reduce the language-specific innate machinery to a conceptual minimum. While the Minimalist Program has helped to sharpen the picture of what features we should attempt to identify in the brain, there is clearly a long way to go. Greater insight into the relationship of linguistic competence to performance (both in the mature and developing grammar) provides the basis of potentially fruitful research into these topics.

Acknowledgements

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