The neurobiology of sentence production

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2025

Abstract

Although there is a sizeable body of literature on sentence comprehension and processing both in healthy and disordered language users, the literature on sentence production remains much more sparse. Linguistic and computational descriptions of expressive syntactic deficits in aphasia are especially rare. In addition, the neuroimaging and (psycho)linguistic literatures operate largely separately. In this paper, I will first lay out the theoretical lay of the land with regard to psycholinguistic models of sentence production. I will then provide a brief narrative overview and large-scale meta-analysis of the neuroimaging literature as it pertains to syntactic computation, followed by an attempt to integrate the psycholinguistic models with the findings from functional and clinical neuroimaging. Finally, I provide a brief overview of the literature surrounding expressive syntactic deficits and propose a path forward to close some of the existing gaps.

1 Introduction

The hierarchical complexity and recursion of human language (i.e., syntax) represent a uniquely human ability. Because of this uniqueness to human cognition, decades of research in both language and cognitive science have investigated the computational architecture and neural substrate of the syntactic system. While syntax is critical both for generating and comprehending complex sentences, it seems to be impossible to fully isolate syntax from other linguistic levels due to the structure of the language system as a whole. In comprehension, the physical signal must first pass through a perceptual system. The perceived signal must then be parsed into smaller chunks which in turn form the elements of the reconstructed syntactic hierarchy for the sentence (Matchin and Hickok, 2020). In production, the syntactic structure generated for a sentence must pass through (at least) the phonological and motor systems before it can be observed. In addition, both comprehension & production are subject to available cognitive and working memory resources (Miller and Chomsky, 1963; Miller, 1965; Hsu et al., 2017). Even at a theoretical level, delineating what is *syntactic* from what is *lexical* (Bates and Goodman, 1997; Fedorenko et al., 2012; Rezaii

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et al., 2022; Le Normand and Thai-Van, 2022) or *semantic* (Skeide et al., 2014; Pylkkänen, 2016) can be challenging across accounts (Pietroski, 2018).

The language sciences as a whole have not yet converged on an agreed-upon definition of syntax. I 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. I concede that although the very notion of a *word* or *lexical item* can be problematic and varies between accounts(Haspelmath, 2017; Murphy, 2024b), it remains a useful shorthand for describing atomic elements of language at a given level of representation.

2 Representational & computational basis of expressive syntax

In this review, I will primarily focus on the *expressive* side of syntax: sentence production. This is not to assert that sentence production and comprehension do not share computational processes or resources *per se*. Such supramodal resource sharing remains possible, however it is incontrovertible that the psycholinguistics and neurobiology of sentence production have been the subject of far less study than of sentence comprehension (Walenski et al., 2019). In particular, the goal of this work is to integrate functional and clinical work into a new and comprehensive review on the neurobiology of sentence production.

A variety of accounts exist which propose architectures for sentence production at the psycholinguistic and/or neural level. In order to make my way through this landscape of theoretical accounts, I have organized the first part of this paper following Marr's (1982) levels of analysis. It should be noted that not all of these accounts make explicit or specific claims aligning to Marr's levels, or even draw distinctions between the different levels (e.g.: collapsing Representation and Algorithm into a single level). Nonetheless, structuring the review around this framework helps illustrate differences between accounts at different levels of abstraction. Within these theories of sentence production, I will be honing in on the claims about the syntactic/structural level of sentence production, leaving semantics/concept generation as well as the phonetic and motor aspects of sentence production for others to address (Levelt, 1989; Pickering and Garrod, 2013). Morphology and morphosyntax are handled differently by the various models, so I will try to address that where applicable. Later on, I will provide a survey of the extant literature regarding the neurobiology of syntactic processing. In the section following that, I will make an attempt to walk through how each of these accounts explains the emergence of observed expressive syntactic disorders like agrammatism and paragrammatism (Heeschen and Kolk, 1988; Matchin et al., 2020). Admittedly, not all of these accounts make direct claims about one or both of these conditions. I will then provide a brief comparison of these models to the available neural data from functional imaging and aphasia, and close by highlighting some gaps and proposing a tentative path forward to fill them. Figure 1 depicts a visual summary of the theoretical accounts outlined in more detail in the rest of this paper at the representational, algorithmic, and hardware levels.

2.1 Computation

Marr's first level is that of Computation: at this level, models must specify the goals of the computation in mapping one kind of information to another (Marr, 1982). The extant models of the neurobiology of syntax do not vary much at this level: they all accept unordered abstract linguistic atoms (which we will take a closer look at in Representations below, as these vary between accounts) and output a linear string consistent with the grammar of the language being used which can then be executed as a motor plan. In general, models of sentence production start with a pre-structural *conceptualization* (Levelt, 1989) or *message* (Bock and Levelt, 1994; Matchin and Hickok, 2020; Krauska and Lau, 2023) level in which the speaker decides what they want to communicate to the listener. For the purposes of this paper, we will assume that this *message* is an unstructured blob of semantic information. There are models which make better-specified claims about this level (cf. Ferreira et al., 2018), but at a linguistic level, this message-generation phase does not fall under the purview of syntax (Pylkkänen, 2019, 2020).
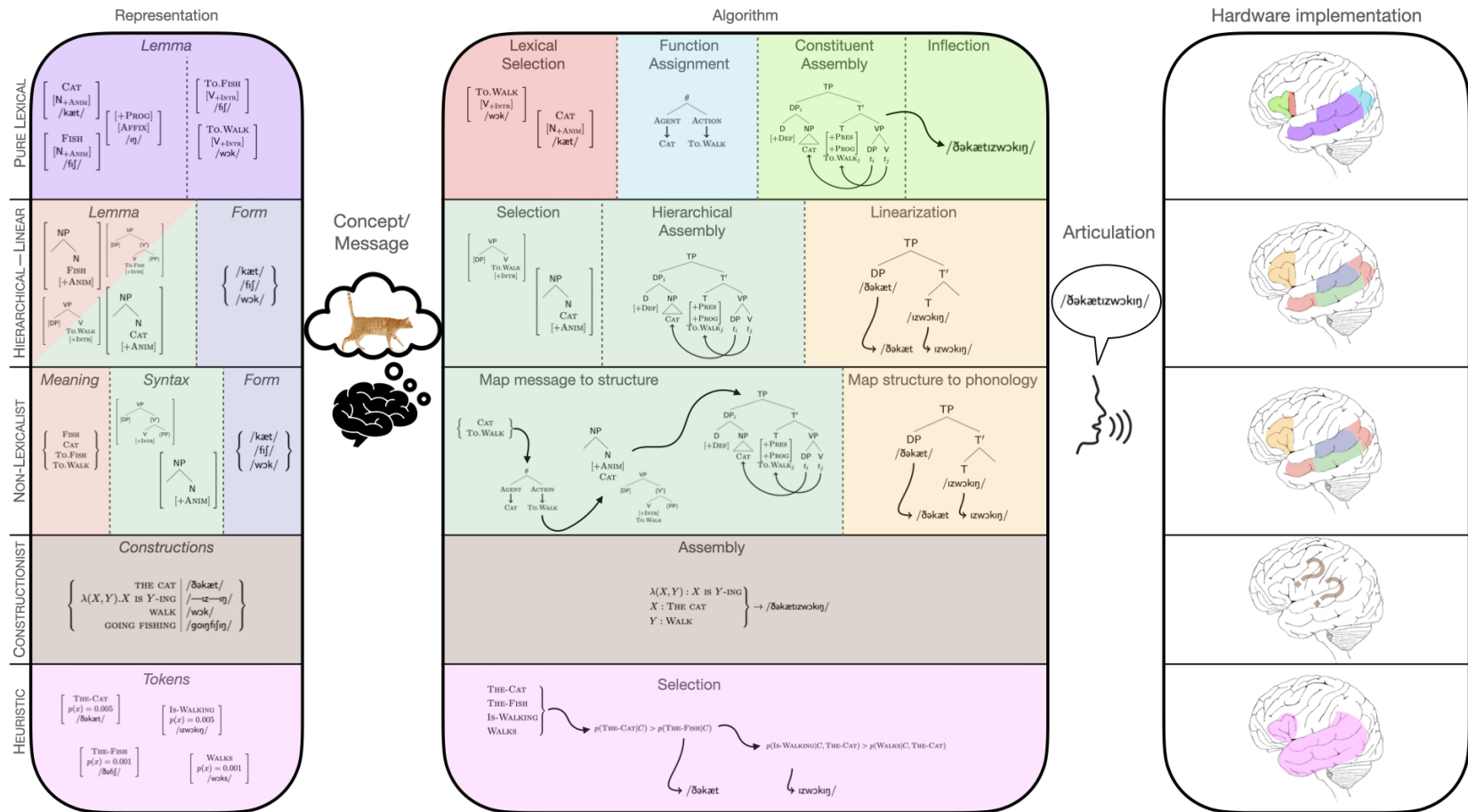
Figure 1: Visual summary of sentence production models organized according to Marr's levels of computation. Each row represents a family of accounts at the representational, algorithmic, and hardware levels. Within the algorithmic level, time unfolds in a roughly left-to-right fashion (depending on amount of parallel computation in that account). Hardware implementation is shown on the brain with ROIs colored matching the representational or algorithmic elements they correspond to.

2.2 Representation

The next level is Representation which addresses the format or data type of the input and output objects. As mentioned above, the input for the models is an unstructured semantic message. The nature of the stored elements of the lexicon (broadly construed) vary between models. The term lexicon has various technical definitions, but I'm using it as a shorthand for stored linguistic knowledge that contains information about word meanings (although the concept of a *word* is problematic in its own right (Haspelmath, 2017; Murphy, 2024b), but is again a convenient shorthand here, rather than a technical term), phonological forms, and low-level structural information. The output form is a phonological string which can be executed as a motor plan, but at this level, too, there are claims about the nature of this string and the mapping between the abstract sounds and motor plan that fall outside the scope of this paper (Dell et al., 2007; Tourville and Guenther, 2011). The accounts essentially differ along two dimensions: the size and nature of the stored units, and the nature of the mechanisms used to combine them.

Pure lexicalist. Under the first account—which I've dubbed the *pure lexicalist* account—the lexicon is composed of *lemmas* (Levelt, 1989; Levelt et al., 1999; Bock and Levelt, 1994; Kemmerer, 2019). Lemmas are 1:1:1 meaning–structure–sound mappings that either contain (Levelt, 1989) or refer to (Levelt et al., 1999; Kemmerer, 2019) the semantic, syntactic, and phonological information for a given word. The lexical entry for the word CAT, for example, would contain references to features of cat-ness, basic syntactic information such as the fact that CAT is a count noun, and references to the sounds /k-æ-t/, either at the phonological or syllabic level (Dell et al., 2008; Biran and Friedmann, 2012). Lexical entries contain information about what kinds of arguments they require and roles they assign (Bock and Levelt, 1994). Verbs, in particular, contain information about their need for a subject, direct object, etc. On the other side of this, rules about grammatical operations are stored in long-term procedural memory (Ullman et al., 1997). The representations of these rules contain information about what kinds of atomic units they can accept and the nature of the operations required to join the atoms.

Hierarchical–Linear. The next account—which I've dubbed the *Hierarchical–Linear* account—has similar notions about the lexicon as the pure lexicalist account, however its proponents are less adherent to the "pure" separation of lexical and syntactic information. Under this account, lemmas are minimal syntactic structures—or *treelets* (Hagoort, 2016; Matchin and Hickok, 2020). These treelets can either be associated with a specific wordform (e.g.: a minimal Noun Phrase with CAT as its head, and a direct mapping to /k-æ-t/ and the semantic features of catness), or in a more abstract form that is not associated with a specific word (e.g.: a Noun Phrase which accepts nouns {CAT, HORSE, GUINEA PIG, etc.} as its head, but which contains the same syntactic information over this class of nouns). These treelet lemmas also contain information about how they might

combine with other treelets to form more complex structures (Hagoort, 2016; Matchin and Hickok, 2020).

Non-lexicalist. Under the non-lexicalist account of syntax, conceptual meanings/messages are stored separately from basic elements of syntactic structure which are in turn stored separately from sound representations (Krauska and Lau, 2023). Each of these levels (meaning, structure, phonology) has its own atomic elements, and there is no 1:1:1 mapping of the elements between levels. Atoms of meaning exist separate from their relationship to structural elements (i.e.: some meaning could map onto multiple structural forms), and there might be multiple structural elements which could be used to construct the same message. Neither messages nor structures have deterministic phonological form, which throws out the concept of the lexicon and lemma and blurs the lines between morphology and syntax.

Constructionist. Under the next family of theories—*Constructionist* accounts—linguistic structures of all levels are stored as units (so-called *constructions*) with built-in rules for how they can combine with other constructions to build out an utterance (Goldberg and Suttle, 2010). These constructions resemble lemmas in some ways, however they eschew notions like parts of speech or types of phrases. As such, there is no verb phrase, only an EAT or a PUT construction which tightly binds structure, meaning, and form. Furthermore, constructions can range in size/scope from a single morpheme to a full sentence construction (Bhattasali et al., 2019; Fukumura and Yang, 2024). There is no separate set of rules for arranging these constructions, but instead the constructions contain the rules to organize themselves. Critically, constructionist accounts generally do not propose a separation between syntax and the lexicon (Goldberg and Suttle, 2010; Deppermann, 2011).

Heuristic. The last account effectively forgoes hierarchical syntactic composition in favor of a more *heuristic* or *usage-based* approach to sentence generation (Ibbotson, 2013). Under these accounts, lexical items are stored as integrated semantic-phonological objects, with minimal to no syntactic or structural information. These objects are stored with information about their transitional probabilities or lexical statistics which determine their use in sentence production, rather than a set of hierarchical syntactic rules *per se* (Behrens, 2009). One version of this is "good-enough" production (e.g., Goldberg and Ferreira, 2022), where speakers will sometimes select sub-optimal forms due to easier access to more frequent or otherwise more salient forms, rather than strictly adhering to the selectional restrictions of the unfolding utterance.

2.2.1 Main points of contention

The main disagreements at this level are the nature of what is stored in memory and the relationships between semantic, syntactic, and phonological information. One option—supported by

the pure lexicalist, heuristic, and constructionist camps—proposes that at least phonological and semantic information are stored as a unit (or at least with a 1-to-1 mapping), with some question about whether structural information is stored in that unit as well. On the other hand, the Hierarchical–Linear and Non-Lexicalist camps propose that each of these levels is stored (at least somewhat) distinctly from the others. In terms of the nature of the items being stored, the non-lexicalist & hierarchical–linear camps tend to assert that there are atomic syntactic objects and/or that lexical items are stored in some sort of minimal syntactic format that does not necessarily map to form. The pure lexicalist and heuristic camps on the other hand tend to argue that syntax is separate from the lexicon and that the words or lexemes being stored are more oriented around form–meaning mappings.

2.3   Algorithm

At the next level of analysis, models must describe the algorithm by which inputs are transformed to outputs (Marr, 1982). In the context of sentence production, at this level, the theories must describe how the relevant representational units are selected & retrieved from memory, as well as specify the rules governing how those units are combined in hierarchical and/or linear structures.

Pure lexicalist.   Under the pure lexicalist account, lemmas or lexical items are transformed into a linear sequence through two sequential processes (see Thompson et al. (2015) and Ferreira et al. (2018) for reviews). The first process is *lexical selection*. In this phase, the appropriate lemmas to convey the message are identified and retrieved from long-term memory (Bock and Levelt, 1994; Kemmerer, 2019). Once they have been retrieved, they undergo the next phase which is *function/relational assignment*, where the lexical items are assigned grammatical roles and syntactic functions (Bock and Levelt, 1994; Ferreira and Slevc, 2007; Fukumura and Yang, 2024). Following function assignment, items must undergo two phases of positional processing: constituent assembly and inflection (Bock and Levelt, 1994; Levelt, 1989; Chang et al., 2006). In constituent assembly, as the syntactic properties of words are consecutively retrieved, they trigger the construction of a surface structure—a sequentially, hierarchically, and relationally organized configuration of syntactic categories (Kemmerer, 2019; Dell and Chang, 2014). In inflection, this newly assembled surface structure is then mapped to the relevant phonological forms by accessing and retrieving the necessary forms corresponding to the lemmas from long-term memory, as well as the phonological forms corresponding to abstract syntactic elements (Bock and Levelt, 1994; Levelt, 1999).

The mechanism for creating progressively larger syntactic structures depends on the nature of lemmas or lexical items in the theory. Under some accounts, lemmas contain some rule-like information (e.g.: selectional restrictions for arguments), whereas in others, structure building happens via a binary joining function like Merge (Zaccarella et al., 2017; Friederici, 2018) or Unify

(Hagoort, 2016, 2017) that joins two typed elements (e.g.: DP + NP). In other words, under some accounts, the syntactic joining rules are contained within the lexical items, whereas in others, the syntactic joining rules are stored separately.

Hierarchical–Linear. The Hierarchical–Linear account has much in common with the lexicalist account in terms of overall architecture. Under the Hierarchical–Linear account, treelet lemmas (or syntactic frames) corresponding to the intended message are retrieved from memory and iteratively assembled into an unordered hierarchical structure (Hagoort, 2017; Matchin and Hickok, 2020). This structured hierarchy is then passed to a linearization module which assigns phonological forms to structural elements (e.g.: tense agreement), and retrieves the phonological forms for the employed treelets from memory. This module then creates a linear sequence of phonological elements which incorporates the structure of the hierarchy with functional morphosyntax (Matchin and Hickok, 2020).

Non-lexicalist. The central point of the non-lexicalist account is that there is no distinction between structural and lexical processes. Under this account, the alogorithm for sentence production is posited in distinct but interacting silos of processing: representation and linearization (Krauska and Lau, 2023). On the representation side, the abstract message is mapped onto the most appropriate syntactic structures. These structures are in turn mapped to phonological forms which are passed to the linearization side to be integrated with pre- and post-syntactic prosodic planning (Ferreira and Humphreys, 2001).

Constructionist. Under the constructionist account, constructions—which can vary in size from single morphemes to full sentence structures—are retrieved from memory and assembled according to their self-contained rules. Constructions are selected on the basis of accessibility which is positively influenced by relevance, appropriateness, frequency, and priming and is negatively influenced by noise, interference, competition, and time pressure (Goldberg and Ferreira, 2022). Accessed/retrieved constructions are *unified* to build up the structure of the sentence (Steels and De Beule, 2006).

Heuristic. Under the heuristic approach, language is more oriented around semantic composition rather than hierarchical syntax (Fedorenko et al., 2016; Mollica et al., 2020). Under this heuristic, usage-based approach, sentences are assembled by minimizing the next-word surprisal in a sentence, rather than forming a top-down hierarchical structure (Rajkumar et al., 2016; Gibson et al., 2019; Hahn et al., 2022). Uniform information density—the concept that information is conveyed at a roughly uniform rate during language production—provides a compelling explanation for the observed data, proposing a rational speaker who manages information rate strategically in response to a noisy communication channel (Frank and Jaeger, 2008; Futrell, 2023b,a). This account relies on

the notion of tokens—phonological forms with a fixed meaning—which are problematic to account for in languages where wordhood is difficult to define (Krauska and Lau, 2023; Murphy, 2024b).

2.3.1 Main points of contention

Naturally the points of contention at this level relate to the differences in representation, but also in the assumptions about on-line generation and underlying non-linear hierarchical structure. Under the Pure Lexicalist, Hierarchical–Linear, and Non-Lexicalist accounts, underlying syntactic structure is (or at least can be) built up into an abstract, non-linear, hierarchical tree. The Constructionist account has some elements of this, but with a blurrier division of labor between syntax, semantics, and lexical statistics. The Heuristic account maintains that no hierarchical structure is built on-line, but rather the order that words appear in an utterance is reliant on learned lexical statistics. A separate debate exists about whether these processes unfold in a serial or parallel fashion over the time course of an utterance (Petersson and Hagoort, 2012; Brehm et al., 2022). Furthermore, accounts differ in the domain-specificity of their components. Some in the Hierarchical–Linear camp assert that the Unifying operations involved in sentence production are supralinguistic (Hagoort, 2016), while most others in the Pure Lexicalist, Hierarchical–Linear and Non-Lexicalist camps contend that syntactic joining operations are a purely linguistic computation. Those in the Constructionist camp would probably agree that constructions—and the built-in operations to join them—are language-specific. In the extreme of the Heuristic account, however, language production can be argued to be supported by domain-general statistical learning and motor chunking (Skinner, 1957; Bybee, 2006), whereas in more moderate interpretations, the lexical statistics are just soft implementations of language-specific syntactic rules (Futrell, 2023b).

3 The brain basis of expressive syntax

Before getting into the proposals regarding Marr's last level—Hardware implementation—corresponding to each of these accounts, I will first provide a brief survey of the extant claims regarding the neurobiology of syntax (Yeaton, 2022). The existence of a large fronto-temporo-parietal language network is at this point a scientific consensus (Geschwind, 1970; Nasios et al., 2019; Lipkin et al., 2022). This neural 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; Matchin et al., 2022a; Uddén et al., 2022). The question then lies in which parts of this network are responsible for the generation of hierarchical syntactic structures (if your theory allows for such a separation; Fedorenko et al., 2020; Shain et al., 2024). Although there is evidence that this network interacts with the basal ganglia to carry out the requisite computations (Barbas et al., 2013; Moreno et al., 2018; Murphy et al., 2022; Turker et al., 2023), I will focus here on the cortical elements of this network which have been posited to play a role in expressive

syntax. Unfortunately, the majority of the empirical work that has been done to date on the neural basis of syntax has been focused on comprehension rather than production (Walenski et al., 2019; LaCroix et al., 2021) due to a long-standing assumption that production and comprehension rely on the same neural architecture and/or due to methodological constraints on language production in functional neuroimaging (Giglio et al., 2022). Broadly speaking, the candidates for a cortical hub for hierarchical, compositional syntactic processing and construction are the Inferior Frontal Gyrus (IFG), anterior temporal lobe (ATL), posterior temporal lobe (PTL), the inferior parietal lobe, the white matter tracts connecting these regions, or all of them together.

Inferior frontal lobe. The first (and most popular) area proposed to be the syntactic hub is the Inferior Frontal Gyrus (IFG). The IFG (in whole or in part) includes Broca's area (Broca, 1861a,b). Broca's area is therefore often used as a stand-in for the IFG, despite Broca's area being a nebulous (Tremblay and Dick, 2016), functionally (Xiang et al., 2010; Rogalsky et al., 2015; Fedorenko and Blank, 2020; Papitto et al., 2020) and architectonically (Anwander et al., 2007; Amunts and Zilles, 2015; Zilles and Amunts, 2018) non-uniform region. The IFG and its sub-components the Pars Triangularis (IFG$_{tri}$) and Pars Opercularis (IFG$_{op}$) have been implicated in a wide variety of linguistic studies targeting complex syntactic structure (Rodd et al., 2015; Uddén and Männel, 2018; Uddén et al., 2022), but which focus predominantly on comprehension (Walenski et al., 2019; Giglio et al., 2022; Riva et al., 2023).

In sentence production, activation of the IFG has been associated with syntactic complexity (Indefrey et al., 2001, 2004), completeness (Grande et al., 2012), and constituent size (Giglio et al., 2022, 2024b), as well as processing load (Menenti et al., 2011). It also shows greater activation for sentence production than word production (Hu et al., 2023) and for sentence production relative to sentence comprehension (Arvidsson et al., 2024), show anticipatory structure building in both production & comprehension (Giglio et al., 2024a). Patients with stroke-induced damage to the IFG present with telegraphic speech (Matchin et al., 2020, 2022a) or generally morphosyntactically reduced output (Schönberger et al., 2014; den Ouden et al., 2019; Gleichgerrcht et al., 2021; Beber et al., 2024). In a longitudinal sample of participants with primary progressive apraxia of speech (Whitwell et al., 2017) or dementia (Ash et al., 2019), participants with more atrophy to frontal regions saw progression to agrammatic primary progressive aphasia (PPA), and this region is prototypically atrophic in patients with non-fluent/agrammatic variant PPA (Matias-Guiu et al., 2019; Lorca-Puls et al., 2024). Patients with PPA-related atrophy to inferior and middle frontal regions show persistent syntactic errors in production (Wilson et al., 2010). 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), and appears to be recruited in the production of grammatical determiners (Ishkhanyan et al., 2020). 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 alone is not sufficient to induce Broca's aphasia (Turken and Dronkers, 2011; Fridriksson et al., 2015; 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 (Fridriksson et al., 2007; Mesulam et al., 2015; Fridriksson et al., 2018). Other non-syntactic proposals for the role of the IFG in sentence production include domain-general cognitive control (Assem et al., 2022), phonological short-term memory (Rogalsky et al., 2008; Mandelli et al., 2016), and lexical selection (Novick et al., 2010; Conner et al., 2019).

Anterior temporal lobe. The next candidate region is the anterior temporal lobe (ATL). Although the general consensus in the field at this point is that the ATL is responsible for conceptual-semantic rather than syntactic composition (Pylkkänen and Brennan, 2020), it has been shown to be active during sentence comprehension and other tasks requiring the composition of meaning (Brennan and Pylkkänen, 2012; Blanco-Elorrieta et al., 2018; Sheng et al., 2019), and for this activity to correlate with parsing steps in computational hierarchical grammars (Bhattasali et al., 2019). Activity in ATL is also higher in comprehension than production during conversation, pointing to a role in sentence comprehension more so than production (Arvidsson et al., 2024). Damage to the ATL, however, seems only to give rise to semantic difficulties rather than syntactic ones (Mesulam et al., 2015; Wilson et al., 2014b; Rogalsky et al., 2018; Stark et al., 2019).

Posterior temporal lobe. The next regions of interest lie in the posterior temporal lobe—the posterior superior and middle temporal gyri (pSTG & pMTG, respectively) and the posterior superior temporal sulcus (pSTS). This is the site of Wernicke's area (Wernicke, 1874), but much like Broca's, Wernicke's area remains ill-defined (Tremblay and Dick, 2016). Activity in the posterior temporal lobe has been shown to correlate with both sentence production & comprehension (Walenski et al., 2019; Matchin and Wood, 2020), and is sensitive to constituent size (Giglio et al., 2022, 2024b), anticipatory structure building (Giglio et al., 2024a), and verb complexity (Takashima et al., 2020) during sentence production. Recent intracranial evidence has found that pMTG and pSTS are sensitive to composition and violations in basic syntactic structures in comprehension (Murphy et al., 2024), and that electrical or magnetic stimulation of posterior temporal sites impacts canonical and non-canonical sentence comprehension (Kyriaki et al., 2020; Riva et al., 2023).

Damage to the posterior temporal lobe is associated with impaired complex sentence comprehension (Biondo et al., 2024; Fahey et al., 2024), and production (Lukic et al., 2021)—especially resulting in paragrammatic speech (Yagata et al., 2017; Matchin et al., 2020; Yeaton et al., 2024). Patients with logopenic variant PPA—a condition typically associated with posterior temporal lobe atrophy, and which has expressive agrammatism as an exclusion criteria (Gorno-Tempini et al., 2011)—saw a reduction in the amount of grammatically correct sentences produced, although the authors did not characterize this non-agrammatic reduction of grammaticality as paragrammatism

(Ash et al., 2019). Damage to the posterior temporal lobe appears to impact thematic role processing, but not morphosyntactic operations (Beber et al., 2024). The storage of the lexicon or lemma system has also been posited in the posterior temporal lobe (Hickok and Poeppel, 2004, 2007) which is consistent with observations from functional imaging in both adults (Menenti et al., 2011, 2012; Grande et al., 2012) and developing children (Vissiennon et al., 2017), as well as evidence from TMS (Krieger-Redwood and Jefferies, 2014) and aphasia (Dronkers et al., 2004) that lesions to the pMTG 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, at least if your theory supports such a distinction). In addition to its linguistic functions, the posterior temporal lobe—especially the superior temporal sulcus—is implicated in theory of mind, face processing, and audiovisual integration (Hein and Knight, 2008).

Inferior parietal lobe. Moving just posteriorly to the posterior temporal lobe, the next candidate is the inferior parietal lobe. It has been argued to support phrase (but not sentence) composition (Williams et al., 2017), and support verb-argument processing (Malyutina and den Ouden, 2017; Takashima et al., 2020), which might be semantic or syntactic depending on your theory. Despite the questionable nature of the inferior parietal lobe's involvement in expressive syntax, there is little doubt that it plays a central role in semantic processing and memory (Binder and Desai, 2011; Price et al., 2015; Schell et al., 2017).

White matter tracts. The last "region" of interest is the white matter connections between posterior temporal and inferior frontal cortex, in particular the arcuate fasciculus (Petersson and Hagoort, 2012; Friederici, 2018; Baboyan et al., 2021). Functional connectivity between inferior frontal and posterior temporal regions has been shown to correlate with syntactic performance in development (Vissiennon et al., 2017). White matter damage to the dorsal tracts connecting these two regions has also been shown to correlate with expressive and receptive syntactic deficits (Fridriksson et al., 2007; Gajardo-Vidal et al., 2021; Gleichgerrcht et al., 2021; Matchin et al., 2022b; Wilson et al., 2011; Bonakdarpour et al., 2019; den Ouden et al., 2019), even when controlling for neighboring gray matter damage.

3.1 Meta-analysis of the neuroimaging literature

To complement the cursory review above of the neural basis of syntax production, I carried out a large-scale meta-analysis of the language neuroimaging literature. Although the pre-trained NeuroSynth database available online (`https://neurosynth.org/`; Yarkoni et al., 2011) contains some language-related keywords, its focus is on the human neuroimaging literature as a whole, rather than just neuroimaging of language. As such, the search terms relevant to this work are relatively few. In order to overcome this problem, I generated a new corpus of neuroimaging
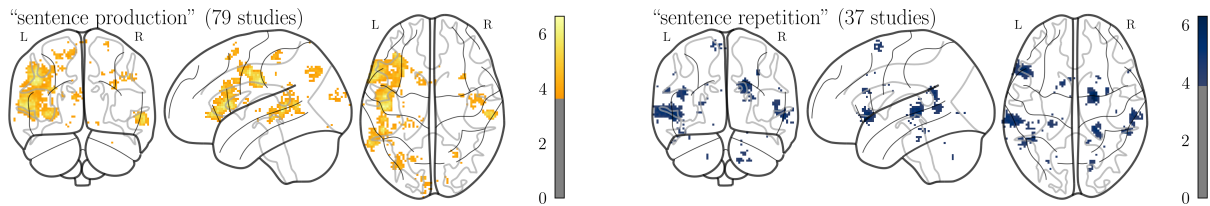
Figure 2: NeuroSynth meta-analytic association map of regions associated with the search term *sentence production* (left) and *sentence repetition* (right). Maps are thresholded at $p < 0.01$.
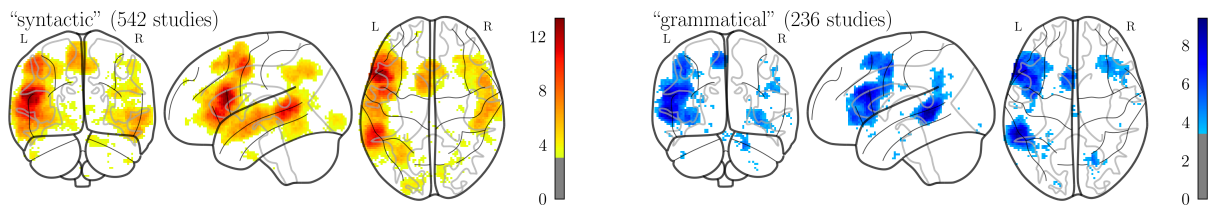

Figure 3: NeuroSynth meta-analytic association map of regions associated with the search term *syntactic* (left), and *grammatical* (right). Maps are thresholded at $p < 0.01$.

literature centered around language, rather than the whole of cognition. In order to do so, I queried[1] PubMedCentral on Nov. 20, 2024 for all articles which report standardized neuroimaging coordinates, and contained the terms *language* or *linguistic* [2]. This resulted in a corpus of more than 2,000 articles from the language neuroscience literature.

Because NeuroSynth generates statistical maps for terms according to relative document frequency, language-relevant keywords are much more frequent in this new corpus, allowing for more interesting insights. The statistical maps generated by NeuroSynth show locations where activation is more consistently reported for studies that mention a given keyword than those that do not (Yarkoni et al., 2011). Unfortunately, however, *syntactic production* was not a common enough term in the literature to generate a statistical map.

On the other hand, both *sentence production* and *sentence repetition* show a significant relationship with posterior temporal regions, as well as inferior frontal cortex (Fig. 2). The map for *sentence production* also shows a relationship with pre- and post-central somatosensory and motor cortex, as well as a smattering of other spots across both hemispheres. The regions of somatosensory and motor cortex implicated by these terms are known to be involved in speech sequencing (Hickok et al., 2014), as well as low-level sensorimotor transformations (Buchsbaum et al., 2011), which makes sense given that the term addresses *sentence production*—which includes other elements of

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[1] Full query term for PMC: (language processing OR language development OR language acquisition OR autism OR ASD OR psycholinguistic OR neurolinguistic OR morphosyntax OR morphosyntactic OR syntax OR syntactic OR phonological OR phonology OR composition OR semantic OR morphological OR phonetic OR sentence OR phrase OR phonemic OR phrase structure OR aphasia OR dementia OR apraxia of speech OR speech OR dld OR sli OR alzheimer OR PPA) AND (language OR linguistic) AND (imaging OR MRI OR fnirs OR MEG OR voxel OR sEEG OR intracranial)

[2] The complete query, dataset, and code are available on the Open Science Framework: `https://osf.io/2f9yc/`
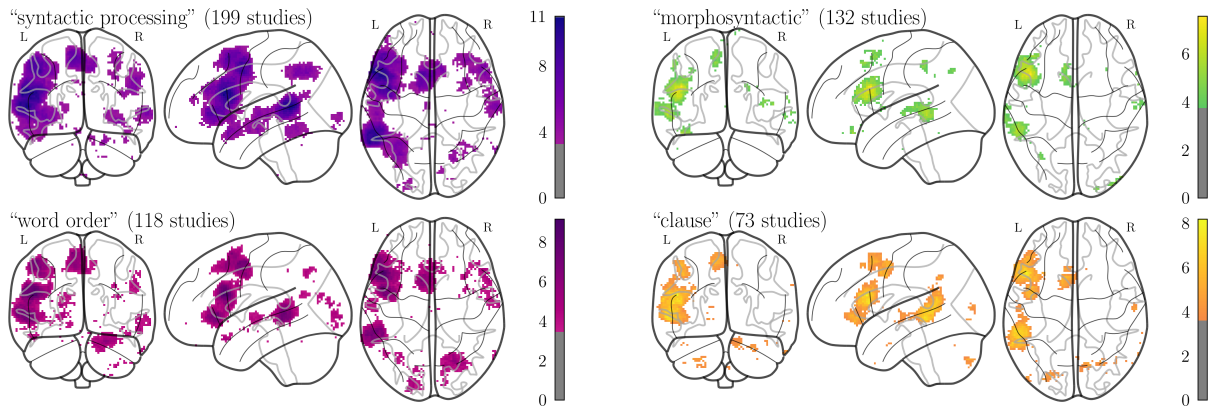
Figure 4: NeuroSynth meta-analytic association map of regions associated with the search term *syntactic processing* (top left), *morphosyntactic* (top right), *word order* (bottom left), and *clause* (bottom right). Maps are thresholded at $p < 0.01$.
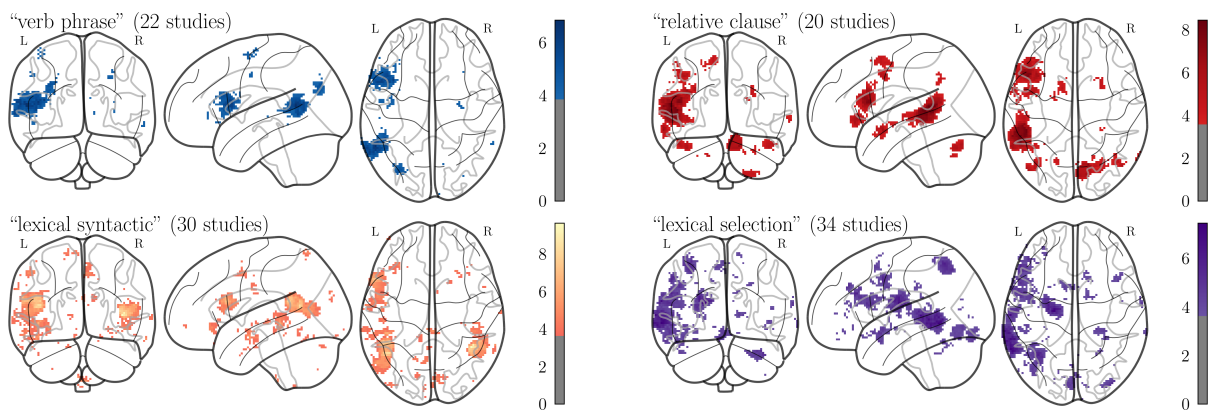

Figure 5: NeuroSynth meta-analytic association map of regions associated with the search term *verb phrase* (top left), *relative clause* (top right), *lexical syntactic* (bottom left) and *lexical selection* (bottom right). Maps are thresholded at $p < 0.01$.

speech planning and production—rather than *syntactic generation.*

Broad strokes syntax terms like *syntactic* or *grammatical* may provide some guidance as to where syntactic computation may be taking place, however these terms do not distinguish between expressive and receptive syntax or grammar (Fig. 3). Other clues may come from other syntax-related terms (e.g., *syntactic processing, morphosyntactic, word order, clause*), which might provide some additional suggestions as to the localization of computational or processing resources (Fig. 4). All of these terms show a significant relationship with inferior and middle frontal regions, as well as with the pSTS or pMTG.

Another set of interesting results are from syntax-related terms that dig into specific structures (e.g., *verb phrase, relative clause*) or terms which straddle the line between syntax and the lexicon (e.g.: *lexical syntactic, lexical selection*).
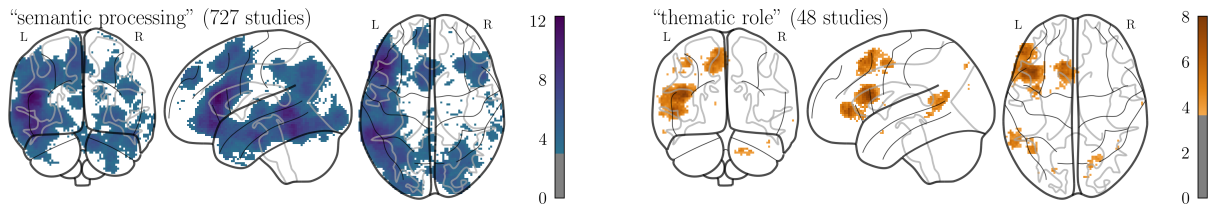
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Figure 6: NeuroSynth meta-analytic association map of regions associated with the search term *semantic processing* (left), and *thematic role* (right). Maps are thresholded at $p < 0.01$.

Even some lexical or verb-related terms might provide some insight due to the close relationship between the lexicon and syntax highlighted by the models discussed in this paper. Indeed, terms like *lexical selection* and both *verb phrase* and *verb naming* show a significant relationship with the pSTS and/or pMTG. All of these terms, as well as *lexical retrieval* show a significant relationship with the inferior frontal lobe, and the two lexical terms also show a relationship with the middle frontal gyrus (Fig. 5, top).

Thus, despite the drawback of this meta-analytic approach (i.e., sentence and syntactic production are not widely reported on in the literature), it provides additional evidence as to the localization of the hardware implementation of the theoretical models discussed in this paper. It does not, however, provide much insight into whether or not a dissociation can be made between syntactic parsing and generation (Momma and Phillips, 2018; Giglio et al., 2022).

3.2 Hardware implementation

Marr's hardware implementation level addresses how the representations and algorithms outlined above could be realized physically (Marr, 1982). While there are some accounts of the neurobiology of syntax which go all the way down to the single cell level (e.g.: Murphy, 2024a), I will focus on the macro level, mapping elements of the high-level algorithms onto regions of cortex, rather than diving deep into the cellular-level dynamics. That said, it is important to note that at the cellular level, we have little to no idea what a *lemma* or *treelet* would be (Poeppel and Idsardi, 2022) which makes it challenging to know what we're mapping at the cortical level (Poeppel, 2012). Nonetheless, Embick and Poeppel (2014) lay out three ways computational theories of language (as those laid out above) can be related to neurobiological evidence: 1) Correlational, in which neural evidence is correlated with some theory, 2) Integrated, in which neural data can help select between computational theories, and 3) Explanatory, in which neural data explains the nature of a computational theory. The data I present here are only used in the first two ways: neural data correlated with linguistic computation to help select between computational theories, especially as they pertain to distribution of labor for different algorithmic processes across different regions (but see Fitz et al., 2024, for a framework on stronger integration between neural and computational

theories in cognitive neuroscience).

It should also be noted that not all accounts outlined above propose relationships between specific operations or representations and locations in the brain. I have excluded the Constructionist camp from this and later sections because I was not able to find any work specifically addressing the localization of the neural basis of constructionist approaches to sentence production, in aphasia or otherwise.

Pure lexicalist. The pure lexicalist account provides specific claims about the localization of the various aspects of the algorithm in the brain (Roelofs and Ferreira, 2019; Roelofs, 2022). On the memory side, lemmas/lexical items are primarily stored in the posterior temporal lobe (Takashima et al., 2020). Lexical selection from a set of candidates is carried out by the inferior frontal cortex (Conner et al., 2019; Zyryanov et al., 2020). The localization of constituent assembly and inflection have less consensus in this camp. Some propose that all of the computations occur in the inferior frontal cortex (Zaccarella and Friederici, 2015; Friederici, 2016, 2020). Others separate constituent assembly and inflection into the posterior temporal lobe and inferior frontal lobe respectively (Wilson et al., 2014a), while still others place all computation in the posterior temporal lobe, with inferior frontal cortex relegated to a cognitive control or monitoring role (Novick et al., 2010; Assem et al., 2022).

Hierarchical–Linear. The hierarchical–linear account suggests a fairly straightforward distribution of labor, mapping the elements of their algorithmic model to patches of cortex (Matchin and Hickok, 2020). Conceptual-semantic information is broadly distributed across the language network, however access nodes are located in anterior middle temporal lobe, and in the angular gyrus in the inferior parietal lobe, following the delineation between entity and event representations put forth by Binder and Desai (2011). The conceptual-semantic elements are combined into hierarchical structures in the pMTG and pSTS. The abstract hierarchical non-linear structures that are built in the posterior temporal lobe are then passed to the inferior frontal lobe (namely the pars triangularis of the IFG) for the morpho-syntactic linearization processes. Murphy (2024a)'s ROSE model proposes a similar cortical distribution of labor with broadly distributed conceptual Representations across the language network, lexical Operations in the pSTS, recursive hierarchical Structures in the pMTG, and linearized Encoding in the inferior frontal lobe.

Non-lexicalist. The main proposal for a non-lexicalist approach to sentence production remains a bit noncommittal about localization in the brain (Krauska and Lau, 2023). They only assert that "the circuit for [mapping message to syntactic structure] is localized to the posterior middle temporal gyrus and superior temporal sulcus, consistent with Matchin and Hickok (2020) and Matchin et al. (2020)." They do not put forth any other proposals regarding the localization of the other elements of their algorithmic model.

Heuristic. The crux of the heuristic account is that no part of the broadly distributed language network is selective to syntax in production or comprehension. The language network—functionally and spatially distinct from domain-general networks like the multiple demand network (Quillen et al., 2021; Shain et al., 2022)—comprises large swaths of fronto-temporo-parietal cortex (Lipkin et al., 2022; Fedorenko et al., 2024), however within this network there is no hub which is uniquely dedicated to syntactic operations (Siegelman et al., 2019; Fedorenko et al., 2020; Hu et al., 2023). Nonetheless, the main proponents of this theory have also produced evidence that morpho-syntactic deficits are localized to the posterior temporal lobe, in line with the other accounts outlined above (Lee et al., 2018, although they did subsequently walk this claim back a bit (Fedorenko et al., 2018)), and that a region in the posterior temporal lobe is sensitive to syntactic structure with or without lexical content (Fedorenko et al., 2012; Shain et al., 2024). These results are challenging to reconcile with their proposed undifferentiated syntactic system.

3.2.1 Main points of contention

With regard to the hardware implementation of syntactic generation, there are two main areas of disagreement. The first is the distributed vs. localized debate. The question here is whether the computational architecture for syntax can be localized to regions of cortex, or whether the system operates on a distributed network of nodes across the language network. The distributed camp argues that because they do not in their fMRI studies find a "syntax-specific" region of activation relative to semantic or lexical variables, then the generative processes proposed by the other camps must not be taking place. Modern generative approaches, however, acknowledge that syntactic and semantic processes are tightly linked, and therefore do not necessarily predict that some syntax specific and selective region should appear in functional imaging over and above semantic operations (Matchin, 2023; Murphy and Woolnough, 2024; Fukumura and Yang, 2024).

The other debate is on the role of Broca's area. On one side are the Broca loyalists—those who maintain that Broca's area is the seat of syntax, and of its Merge operation—and on the other side are those who have shifted towards the temporal lobe (some anterior, some posterior) as the seat of syntactic computation. Even with some over-weighting of evidence from fMRI by the Heuristic camp, the various theorists largely agree that different neuroimaging modalities (e.g.: intracranial, fMRI, lesion studies) provide useful, complementary insights and acknowledge that multimodal evidence accumulation is critical to theory development.

4 Expressive syntactic deficits

It is not only possible, but likely, that multiple of the accounts above are correct in accounting for different aspects of linguistic behavior—some may be more cognitively plausible, while others provide more descriptive power or clarity of formalism. One useful way to distinguish these theories

is to examine them through the lens of aphasia. Can we lend credence to one or another of these theories by looking at how the ability to generate well-formed sentences breaks down following brain damage?

4.1 Types of expressive deficits

There are two main categories of expressive syntactic deficits: agrammatism and paragrammatism. Agrammatism is characterized by "telegraphic" speech which systematically omits functional morphemes (e.g.: *boy kick ball*) but maintains the more informative content words in a sentence (Rezaii et al., 2022, 2023). Paragrammatism, on the other hand, is characterized by *confused sentence monsters*—as Kleist (1914) called them—which contain morphosyntactic insertions, substitutions, and transpositions rather than reductions (Heeschen and Kolk, 1988; Kolk and Heeschen, 1992; Matchin et al., 2020). Although some accounts propose that agrammatism and paragrammatism are two different presentations/adaptations to the same underlying deficit (Heeschen, 1985; Kolk and Heeschen, 1992), we will now look at how these two conditions might arise as distinct syndromes under the models of sentence production introduced above (Yeaton et al., 2025).

4.2 Accounting for these data

Pure lexicalist. Most proponents of the pure lexicalist account tend to subscribe to a very "Broca's area" view of the organization of syntax. As such, expressive agrammatism is caused by a breakdown in the hierarchy building mechanism (e.g., Merge) that is couched in the inferior frontal lobe (Whitwell et al., 2017; Grodzinsky et al., 2021). Another explanation calls back to the distinction between relational processing and constituent assembly in sentence production: relational processing is housed in the temporal lobe while constituent assembly is carried out by the inferior frontal lobe (Biran and Friedmann, 2012; DeLeon et al., 2012). This camp contends that paragrammatism is caused by a breakdown in control processes—rather than in linguistic knowledge or computation—citing evidence that individuals with paragrammatic symptoms make qualitatively similar errors to healthy controls, only at a much higher rate (Butterworth and Howard, 1987; Harley, 1990).

Hierarchical–Linear. Under the Hierarchical–Linear account, agrammatism is caused by a breakdown in the morphosyntactic linearization process which is localized to the frontal lobe (DeLeon et al., 2012; Matchin et al., 2020). Under this account, there is no loss of linguistic knowledge *per se* (Linebarger et al., 1983; Miceli et al., 1983), nor breakdown in hierarchical production ability, but rather a breakdown in translating a hierarchical structure into a linear sequence of morphemes (Wang et al., 2014). The source of paragrammatism is more unclear. The deficits observed in paragrammatic production could reasonably arise either due to a breakdown in hierarchical syntactic knowledge, or a breakdown in forward modeling and monitoring (Fahey et al.,

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2025).

Non-lexicalist. Under the non-lexicalist account agrammatism is caused by a breakdown in post-syntactic and cognitive control processes (Krauska and Lau, 2023). Paragrammatism, on the other hand, is caused by a breakdown in syntactic processes, however the apparent fluency is accounted for by proposing that post-syntactic phonological processes are functioning normally and therefore at least partially able to hide/correct for the breakdowns in the structural phase.

Heuristic. Under the heuristic/usage-based account, agrammatism arises as a resource-rational adaptation to difficulties in lexical access rather than a syntactic deficit (Fedorenko et al., 2022; Faroqi-Shah, 2023). Indeed, analysis of data from agrammatic production shows a tradeoff between syntactic complexity and lexical frequency/informativity (Rezaii et al., 2022, 2023), and strategies have been shown to vary betweeen tasks (Sahraoui and Nespoulous, 2012). Paragrammatism, on the other hand, results from actual loss of linguistic knowledge—the mapping between linguistic forms and the associated meanings (Salis and Edwards, 2004; Fedorenko et al., 2022). It remains unclear, however, how a specific impairment to linguistic/grammatical knowledge could occur in only some cases of brain damage if such knowledge and processing is distributed rather than localized. Furthermore, it is possible, and even likely, that some of the behavior we observe in agrammatism is attributable to economy of effort, but there is no possible economic reason for the emergence of paragrammatism.

4.3 Monitoring & Control vs. Grammatical impairment

Pickering and Garrod (2013) propose a framework for sentence production where speech commands are produced alongside forward models of the production. During speech, then, output is monitored and compared to the forward model to ensure that it is consistent with expectations. This forward modelling approach may help to catch errors before they occur, but may also be used to detect and correct errors once committed. This same framework could apply to sentence production as well—the sentence generation system produces a linear sequence to be sent as a speech plan, which is then monitored and compared to the forward modelled sentence in order to detect errors that may have arisen. Monitoring for errors probably does not do much good if there is no mechanism to arrest and revise the production plan before it is produced (e.g.: Dell et al. (2008)'s "syntactic traffic cop"). For this reason, cognitive control (or lack thereof) may play an important role in production of well-formed sentences.

While it does not seem like monitoring and control play a crucial role in agrammatic production—since most people with expressive agrammatism are aware of their errors online, and often make correction attempts that still fail (Marshall and Tompkins, 1982)— the pattern of errors observed paragrammatism in have been explained under some accounts as a breakdown in the efficacy of

some control module since the errors mirror those observed in healthy speakers, albeit appearing with much greater frequency (Butterworth and Howard, 1987).

A piece of evidence in this debate regarding the role of monitoring and control is *anosagnosia*, or the awareness of one's own deficit (Razafimahatratra et al., 2023). While agrammatic speakers tend to be aware of the errors they commit, it does not seem that all—if any—paragrammatic speakers share this awareness (e.g., Maher et al., 1994), leading to claims that paragrammatism critically involves a lack of awareness of the deficit (W. Matchin, personal communication, Dec. 1, 2023).

5   Gaps and a path forward

Because of the elusive nature of the language system—and of syntax in particular—current psycho- and neurolinguistic methods used to target syntactic processing are confounded by demands on other cognitive and linguistic systems. Such confounds include working memory demands (Baddeley et al., 2009), semantic composition (Malyutina and den Ouden, 2017; Siegelman et al., 2019; Pylkkänen, 2020), and unnatural language conditions (Pylkkänen and Brennan, 2020). Another persistent problem is that studies often address only comprehension under the assumption that production employs the same mechanisms at a computational and neural level (Zaccarella et al., 2017; Friederici, 2018). This raises two questions—one theoretical and the other methodological: 1) What is the relationship between sentence generation and sentence comprehension? and 2) What sort of empirical data would inform our understanding of this relationship?

5.1   So what about comprehension?

Throughout this paper, I have done my best to ignore comprehension, but there are still theoretical and empirical reasons to believe that sentence production and comprehension rely (at least in part) on the same underlying mechanism(s) (Momma and Phillips, 2018; Matchin and Hickok, 2020). In order to fully characterize the sentence production system, it is crucial to understand the relationship between syntactic generation and parsing. There is relatively little work comparing the functional imaging correlates of the two in the same participants. Only a handful of (mostly recent) studies have compared the neural bases of sentence production to those of comprehension (e.g., Indefrey et al., 2004; Segaert et al., 2012; Giglio et al., 2022; Hu et al., 2023; Arvidsson et al., 2024, *inter alia*). These studies consistently find overlap in the neural resources recruited in sentence production and comprehension—especially in the inferior frontal and posterior temporal lobes (Menenti et al., 2011; Segaert et al., 2012; Giglio et al., 2022), as well as a smattering of other sites across the frontal, parietal, and temporal lobes—although commonly with differential levels of activation between production and comprehension (Hu et al., 2023; Giglio et al., 2024a). In PPA, expressive agrammatism is associated with inferior frontal atrophy, while receptive agrammatism is

associated with posterior temporal atrophy (Lorca-Puls et al., 2024). The issue of the relationship between expressive and receptive syntactic competence in post-stroke aphasia is relatively unexplored, at least under targeted investigation. Some work exists which used existing large datasets to probe this question (Lukic et al., 2021; Matchin et al., 2022b, 2023), however these studies were constrained by the available data. Nonetheless, inferior frontal damage appears to induce agrammatic speech, without significant syntactic comprehension deficits (Goodglass and Mayer, 1958; Linebarger et al., 1983; Matchin et al., 2023) (although *sentence comprehension* deficits may still be attested due to reduced working memory or cognitive capacity (Rogalsky et al., 2018)). On the other hand, damage to the posterior temporal lobe seems to induce paragrammatic speech (or at least non-canonical sentence production deficits) *and* cause syntactic comprehension deficits (Matchin et al., 2023), however no systematic investigation has been done to assess the comprehension abilities of participants presenting with paragrammatic speech in either post-stroke aphasia or PPA (Eling et al., 1987; Heeschen, 1985; Yeaton et al., 2023). Furthermore, some models of the neurobiology of aphasia have perpetuated problematic notions about the nature of language disorders, clumping gross patterns of expressive and receptive symptoms into "syndromes" that often do not fit the patterns observed in patients (Marshall and Newcombe, 1988; Brownsett et al., 2019; Landrigan et al., 2021). With regard to the role of control in sentence production, it remains possible that some error monitoring could be carried out by a/the comprehension system rather than a separate monitoring system built into the sentence generation process, assuming such separate systems could exist. Such an investigation is critical in order to understand the distribution of labor underlying syntactic processing.

6 Conclusions

In sum, the theoretical landscape regarding the hierarchical/structural level of sentence production includes a few overlapping or comparable claims, but also some proposals which are mutually exclusive. Some of these accounts present better parsimony with data from expressive syntactic deficits than others, however much work remains to be done in characterizing the relationship between the different levels of syntactic processing.

In order to address these methodological, empirical, and theoretical gaps, more, higher quality and greater depth data is needed. It remains rare to see difficulty-matched tasks assessing both receptive and expressive syntactic competence in the same participants in either functional imaging or lesion studies. Some recent work has started to address this gap by gathering functional imaging or electrophysiological data during naturalistic or constrained sentence production and comprehension (Giglio et al., 2024a). Even relatively constrained sentence production tasks can provide crucial insights into how the dynamics of sentence production differ from those of single word production (Morgan et al., 2024a,b). It is also worth investigating the role that syntax plays in the Sentence Superiority Effect in both healthy and clinical populations (Snell and Grainger, 2017) and how

that might inform our understanding of the neurobiological architecture of syntactic processing (Dufau et al., 2024). The use of electrical or magnetic stimulation investigating syntactic processes (especially in production) is also understudied (see Qu et al., 2022; Ntemou et al., 2023, for recent reviews), which, combined with an individual-subjects localization approach (Fedorenko et al., 2010) may provide critical causal insights into syntactic processes in a more controlled fashion than lesion studies. In terms of future directions from aphasic populations, existing datasets of people with aphasia often do not have tasks assessing sentence comprehension, repetition, and production for the same participants. Furthermore, the tasks used to assess these different processes often use distinct items making it possible that differences in performance on the different tasks could be an artifact of the items used, rather than a dissociation between the syntactic abilities of the participants. On a more soapbox note, it is important that the field moves away from talking about syntactic processing as a monolith, assuming that the same processes are used in both expressive and receptive processes, until further data can be brought to bear on the issue to either support or reject this long-held stance.

References

Amunts, K. and Zilles, K. (2015). Architectonic mapping of the human brain beyond brodmann. *Neuron*, 88(6):1086–1107.

Andrews, J. P., Cahn, N., Speidel, B. A., Chung, J. E., Levy, D. F., Wilson, S. M., Berger, M. S., and Chang, E. F. (2023). Dissociation of Broca's area from Broca's aphasia in patients undergoing neurosurgical resections. *Journal of Neurosurgery*, 1(aop):1–11.

Anwander, A., Tittgemeyer, M., von Cramon, D. Y., Friederici, A. D., and Knösche, T. R. (2007). Connectivity-based parcellation of Broca's area. *Cerebral cortex*, 17(4):816–825.

Arvidsson, C., Torubarova, E., Pereira, A., and Uddén, J. (2024). Conversational production and comprehension: fmri-evidence reminiscent of but deviant from the classical broca–wernicke model. *Cerebral Cortex*, 34(3).

Ash, S., Nevler, N., Phillips, J., Irwin, D. J., McMillan, C. T., Rascovsky, K., and Grossman, M. (2019). A longitudinal study of speech production in primary progressive aphasia and behavioral variant frontotemporal dementia. *Brain and language*, 194:46–57.

Assem, M., Hart, M. G., Coelho, P., Romero-Garcia, R., McDonald, A., Woodberry, E., Morris, R. C., Price, S. J., Suckling, J., Santarius, T., et al. (2022). High gamma activity distinguishes frontal cognitive control regions from adjacent cortical networks. *Cortex*.

Baboyan, V., Basilakos, A., Yourganov, G., Rorden, C., Bonilha, L., Fridriksson, J., and Hickok, G. (2021). Isolating the white matter circuitry of the dorsal language stream: Connectome-symptom mapping in stroke induced aphasia. *Human Brain Mapping*, 42(17):5689–5702.

Baddeley, A., Hitch, G., and Allen, R. (2009). Working memory and binding in sentence recall. *Journal of Memory and Language*, 61(3):438–456.

Barbas, H., García-Cabezas, M. Á., and Zikopoulos, B. (2013). Frontal-thalamic circuits associated with language. *Brain and language*, 126(1):49–61.

Bates, E. and Goodman, J. C. (1997). On the inseparability of grammar and the lexicon: Evidence from acquisition, aphasia and real-time processing. *Language and cognitive Processes*, 12(5-6):507–584.

Beber, S., Bontempi, G., Miceli, G., and Tettamanti, M. (2024). The neurofunctional correlates of morphosyntactic and thematic impairments in aphasia: A systematic review and meta-analysis. *Neuropsychology Review*.

Behrens, H. (2009). Usage-based and emergentist approaches to language acquisition. *Linguistics*, 47(2).

Bhattasali, S., Fabre, M., Luh, W.-M., Al Saied, H., Constant, M., Pallier, C., Brennan, J. R., Spreng, R. N., and Hale, J. (2019). Localising memory retrieval and syntactic composition: An fMRI study of naturalistic language comprehension. *Language, Cognition and Neuroscience*, 34(4):491–510.

Binder, J. R. and Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in cognitive sciences*, 15(11):527–536.

Biondo, N., Ivanova, M. V., Pracar, A. L., Baldo, J., and Dronkers, N. F. (2024). Mapping sentence comprehension and syntactic complexity: evidence from 131 stroke survivors. *Brain Communications*, 6(6).

Biran, M. and Friedmann, N. (2012). The representation of lexical-syntactic information: Evidence from syntactic and lexical retrieval impairments in aphasia. *Cortex*, 48(9):1103–1127.

Blanco-Elorrieta, E., Kastner, I., Emmorey, K., and Pylkkänen, L. (2018). Shared neural correlates for building phrases in signed and spoken language. *Scientific reports*, 8(1):1–10.

Bock, K. and Levelt, W. (1994). Language production: Grammatical encoding. *Handbook of psycholinguistics*, 5:405–452.

Bonakdarpour, B., Hurley, R. S., Wang, A. R., Fereira, H. R., Basu, A., Chatrathi, A., Guillaume, K., Rogalski, E. J., and Mesulam, M. M. (2019). Perturbations of language network connectivity in primary progressive aphasia. *Cortex*, 121:468–480.

Bozic, M., Fonteneau, E., Su, L., and Marslen-Wilson, W. D. (2015). Grammatical analysis as a distributed neurobiological function. *Human brain mapping*, 36(3):1190–1201.

Braga, R. M., DiNicola, L. M., Becker, H. C., and Buckner, R. L. (2020). Situating the left-lateralized language network in the broader organization of multiple specialized large-scale distributed networks. *Journal of neurophysiology*, 124(5):1415–1448.

Brehm, L., Cho, P. W., Smolensky, P., and Goldrick, M. A. (2022). Pips: A parallel planning model of sentence production. *Cognitive Science*, 46(2).

Brennan, J. and Pylkkänen, L. (2012). The timecourse and spatial distribution of brain activity associated with sentence processing. *Neuroimage*, 60(2):1139–1148.

Broca, P. (1861a). Nouvelle observation d'aphémie produite par une lésion de la moitié postérieure des deuxième et troisième circonvolutions frontales. *Bulletins de la Société anatomique de Paris*, 36:398–407.

Broca, P. (1861b). Remarques sur le siège de la faculté du langage articulé, suivies d'une observation d'aphémie (perte de la parole). *Bulletin et Memoires de la Societe anatomique de Paris*, 6:330–357.

Brownsett, S., Ramajoo, K., Copland, D., McMahon, K., Robinson, G., Drummond, K., Jeffree, R., Olson, S., Ong, B., and De Zubicaray, G. (2019). Language deficits following dominant hemisphere tumour resection are significantly underestimated by syndrome-based aphasia assessments. *Aphasiology*, 33(10):1163–1181.

Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D'Esposito, M., and Hickok, G. (2011). Conduction aphasia, sensory-motor integration, and phonological short-term memory–an aggregate analysis of lesion and fmri data. *Brain and language*, 119(3):119–128.

Butterworth, B. and Howard, D. (1987). Paragrammatisms. *Cognition*, 26(1):1–37.

Bybee, J. L. (2006). From usage to grammar: The mind's response to repetition. *Language*, 82(4):711–733.

Caucheteux, C., Gramfort, A., and King, J.-R. (2021). Disentangling syntax and semantics in the brain with deep networks. In *International Conference on Machine Learning*, pages 1336–1348. PMLR.

Chang, E. F., Kurteff, G., and Wilson, S. M. (2018). Selective interference with syntactic encoding during sentence production by direct electrocortical stimulation of the inferior frontal gyrus. *Journal of cognitive neuroscience*, 30(3):411–420.

Chang, F., Dell, G. S., and Bock, K. (2006). Becoming syntactic. *Psychological Review*, 113(2):234–272.

Conner, C. R., Kadipasaoglu, C. M., Shouval, H. Z., Hickok, G., and Tandon, N. (2019). Network dynamics of broca's area during word selection. *PLoS One*, 14(12):e0225756.

DeLeon, J., Gesierich, B., Besbris, M., Ogar, J., Henry, M. L., Miller, B. L., Gorno-Tempini,

M. L., and Wilson, S. M. (2012). Elicitation of specific syntactic structures in primary progressive aphasia. *Brain and language*, 123(3):183–190.

Dell, G. S. and Chang, F. (2014). The p-chain: relating sentence production and its disorders to comprehension and acquisition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1634):20120394.

Dell, G. S., Martin, N., and Schwartz, M. F. (2007). A case-series test of the interactive two-step model of lexical access: Predicting word repetition from picture naming. *Journal of memory and language*, 56(4):490–520.

Dell, G. S., Oppenheim, G. M., and Kittredge, A. K. (2008). Saying the right word at the right time: Syntagmatic and paradigmatic interference in sentence production. *Language and Cognitive Processes*, 23(4):583–608.

den Ouden, D.-B., Malyutina, S., Basilakos, A., Bonilha, L., Gleichgerrcht, E., Yourganov, G., Hillis, A. E., Hickok, G., Rorden, C., and Fridriksson, J. (2019). Cortical and structural-connectivity damage correlated with impaired syntactic processing in aphasia. *Human brain mapping*, 40(7):2153–2173.

Deppermann, A. (2011). *Constructions vs. lexical items as sources of complex meanings: A comparative study of constructions with German verstehen*, page 88–126. DE GRUYTER.

Dronkers, N. F., Wilkins, D. P., Van Valin Jr, R. D., Redfern, B. B., and Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, 92(1-2):145–177.

Dufau, S. E., Yeaton, J. D., Badier, J.-M., Chen, S., Holcomb, P. J., and Grainger, J. (2024). Sentence superiority in the reading brain. *Neuropsychologia*.

Eling, P., de Bot, K., Keyser, A., and Van der Sande, C. (1987). Paragrammatic speech without a comprehension deficit? a case report. *Brain and language*, 31(1):36–42.

Embick, D. and Poeppel, D. (2014). Towards a computational(ist) neurobiology of language: correlational, integrated and explanatory neurolinguistics. *Language, Cognition and Neuroscience*, 30(4):357–366.

Fahey, D., Fridriksson, J., Hickok, G., and Matchin, W. (2024). Lesion-symptom mapping of acceptability judgments in chronic poststroke aphasia reveals the neurobiological underpinnings of receptive syntax. *Journal of Cognitive Neuroscience*, page 1–15.

Fahey, D., Yeaton, J., Stark, B., Fridriksson, J., Den Ouden, D., Hickok, G., and Matchin, W. (2025). An objective coding scheme for grammatical production deficits in aphasia reveals a categorical divide between agrammatism and paragrammatism. PsyArXiv.

Faroqi-Shah, Y. (2023). A reconceptualization of sentence production in post-stroke agrammatic aphasia: the synergistic processing bottleneck model. *Frontiers in Language Sciences*, 2.

Fedorenko, E. and Blank, I. A. (2020). Broca's area is not a natural kind. *Trends in cognitive sciences*, 24(4):270–284.

Fedorenko, E., Blank, I. A., Siegelman, M., and Mineroff, Z. (2020). Lack of selectivity for syntax relative to word meanings throughout the language network. *Cognition*, 203:104348.

Fedorenko, E., Hsieh, P.-J., Nieto-Castañón, A., Whitfield-Gabrieli, S., and Kanwisher, N. (2010). New method for fMRI investigations of language: defining ROIs functionally in individual subjects. *Journal of neurophysiology*, 104(2):1177–1194.

Fedorenko, E., Ivanova, A. A., and Regev, T. I. (2024). The language network as a natural kind within the broader landscape of the human brain. *Nature Reviews Neuroscience*, 25(5):289–312.

Fedorenko, E., Nieto-Castanon, A., and Kanwisher, N. (2012). Lexical and syntactic representations in the brain: an fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia*, 50(4):499–513.

Fedorenko, E., Ryskin, R., and Gibson, E. (2022). Agrammatic output in non-fluent, including broca's, aphasia as a rational behavior. *Aphasiology*, 37(12):1981–2000.

Fedorenko, E., Scott, T. L., Brunner, P., Coon, W. G., Pritchett, B., Schalk, G., and Kanwisher, N. (2016). Neural correlate of the construction of sentence meaning. *Proceedings of the National Academy of Sciences*, 113(41):E6256–E6262.

Fedorenko, E., Williams, Z. M., and Ferreira, V. S. (2018). Remaining puzzles about morpheme production in the posterior temporal lobe. *Neuroscience*, 392:160–163.

Ferreira, V. S. and Humphreys, K. R. (2001). Syntactic influences on lexical and morphological processing in language production. *Journal of Memory and Language*, 44(1):52–80.

Ferreira, V. S., Morgan, A., and Slevc, L. R. (2018). Grammatical encoding.

Ferreira, V. S. and Slevc, L. R. (2007). *Grammatical Encoding*, page 453–470. Oxford University Press.

Fitz, H., Hagoort, P., and Petersson, K. M. (2024). Neurobiological causal models of language processing. *Neurobiology of Language*, page 1–23.

Frank, A. F. and Jaeger, T. F. (2008). Speaking rationally: Uniform information density as an optimal strategy for language production. In *Proceedings of the annual meeting of the cognitive science society*, volume 30.

Fridriksson, J., Bonilha, L., and Rorden, C. (2007). Severe Broca's aphasia without Broca's area damage. *Behavioural neurology*, 18(4):237–238.

Fridriksson, J., den Ouden, D.-B., Hillis, A. E., Hickok, G., Rorden, C., Basilakos, A., Yourganov, G., and Bonilha, L. (2018). Anatomy of aphasia revisited. *Brain*, 141(3):848–862.

Fridriksson, J., Fillmore, P., Guo, D., and Rorden, C. (2015). Chronic Broca's aphasia is caused by damage to Broca's and Wernicke's areas. *Cerebral Cortex*, 25(12):4689–4696.

Friederici, A. D. (2016). The neuroanatomical pathway model of language: Syntactic and semantic networks. In *Neurobiology of language*, pages 349–356. Elsevier.

Friederici, A. D. (2018). The neural basis for human syntax: Broca's area and beyond. *Current opinion in behavioral sciences*, 21:88–92.

Friederici, A. D. (2020). Hierarchy processing in human neurobiology: How specific is it? *Philosophical Transactions of the Royal Society B*, 375(1789):20180391.

Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., and Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral cortex*, 13(2):170–177.

Fukumura, K. and Yang, F. (2024). Interactive structure building in sentence production. *Cognitive Psychology*, 148:101616.

Futrell, R. (2023a). Information-theoretic principles in incremental language production. *Proceedings of the National Academy of Sciences*, 120(39).

Futrell, R. (2023b). An information-theoretic account of availability effects in language production. *Topics in Cognitive Science*, 16(1):38–53.

Gajardo-Vidal, A., Lorca-Puls, D. L., Team, P., Warner, H., Pshdary, B., Crinion, J. T., Leff, A. P., Hope, T. M., Geva, S., Seghier, M. L., et al. (2021). Damage to Broca's area does not contribute to long-term speech production outcome after stroke. *Brain*, 144(3):817–832.

Geschwind, N. (1970). The organization of language and the brain: Language disorders after brain damage help in elucidating the neural basis of verbal behavior. *Science*, 170(3961):940–944.

Gibson, E., Futrell, R., Piantadosi, S. P., Dautriche, I., Mahowald, K., Bergen, L., and Levy, R. (2019). How efficiency shapes human language. *Trends in Cognitive Sciences*, 23(5):389–407.

Giglio, L., Ostarek, M., Sharoh, D., and Hagoort, P. (2024a). Diverging neural dynamics for syntactic structure building in naturalistic speaking and listening. *Proceedings of the National Academy of Sciences*, 121(11).

Giglio, L., Ostarek, M., Weber, K., and Hagoort, P. (2022). Commonalities and asymmetries in the neurobiological infrastructure for language production and comprehension. *Cerebral Cortex*, 32(7):1405–1418.

Giglio, L., Sharoh, D., Ostarek, M., and Hagoort, P. (2024b). Connectivity of fronto-temporal regions in syntactic structure building during speaking and listening. *Neurobiology of Language*, page 1–20.

Gleichgerrcht, E., Roth, R., Fridriksson, J., den Ouden, D., Delgaizo, J., Stark, B., Hickok, G., Rorden, C., Wilmskoetter, J., Hillis, A., et al. (2021). Neural bases of elements of syntax during speech production in patients with aphasia. *Brain and Language*, 222:105025.

Goldberg, A. and Suttle, L. (2010). Construction grammar. *WIREs Cognitive Science*, 1(4):468–477.

Goldberg, A. E. and Ferreira, F. (2022). Good-enough language production. *Trends in Cognitive Sciences*, 26(4):300–311.

Goodglass, H. and Mayer, J. (1958). Agrammatism in aphasia. *Journal of Speech and Hearing Disorders*, 23(1):99–111.

Gorno-Tempini, M. L., Hillis, A. E., Weintraub, S., Kertesz, A., Mendez, M., Cappa, S. F., Ogar, J. M., Rohrer, J. D., Black, S., Boeve, B. F., et al. (2011). Classification of primary progressive aphasia and its variants. *Neurology*, 76(11):1006–1014.

Grande, M., Meffert, E., Schoenberger, E., Jung, S., Frauenrath, T., Huber, W., Hussmann, K., Moormann, M., and Heim, S. (2012). From a concept to a word in a syntactically complete sentence: An fMRI study on spontaneous language production in an overt picture description task. *NeuroImage*, 61(3):702–714.

Grodzinsky, Y., Pieperhoff, P., and Thompson, C. (2021). Stable brain loci for the processing of complex syntax: A review of the current neuroimaging evidence. *Cortex*, 142:252–271.

Hagoort, P. (2016). MUC (Memory, Unification, Control): A model on the neurobiology of language beyond single word processing. In *Neurobiology of language*, pages 339–347. Elsevier.

Hagoort, P. (2017). The core and beyond in the language-ready brain. *Neuroscience & Biobehavioral Reviews*, 81:194–204.

Hahn, M., Futrell, R., Levy, R., and Gibson, E. (2022). A resource-rational model of human processing of recursive linguistic structure. *Proceedings of the National Academy of Sciences*, 119(43):e2122602119.

Harley, T. A. (1990). Paragrammatisms: Syntactic disturbance or breakdown of control? *Cognition*, 34(1):85–91.

Haspelmath, M. (2017). The indeterminacy of word segmentation and the nature of morphology and syntax. *Folia linguistica*, 51(s1000):31–80.

Heeschen, C. (1985). Agrammatism versus paragrammatism: A fictitious opposition. In *Agrammatism*, pages 207–248. Elsevier.

Heeschen, C. and Kolk, H. (1988). Agrammatism and paragrammatism. *Aphasiology*, 2(3-4):299–302.

Hein, G. and Knight, R. T. (2008). Superior temporal sulcus—it's my area: Or is it? *Journal of Cognitive Neuroscience*, 20(12):2125–2136.

Hickok, G. and Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1-2):67–99.

Hickok, G. and Poeppel, D. (2007). The cortical organization of speech processing. *Nature reviews neuroscience*, 8(5):393–402.

Hickok, G., Rogalsky, C., Chen, R., Herskovits, E. H., Townsley, S., and Hillis, A. E. (2014). Partially overlapping sensorimotor networks underlie speech praxis and verbal short-term memory: evidence from apraxia of speech following acute stroke. *Frontiers in Human Neuroscience*, 8:649.

Hiersche, K. J., Schettini, E., Li, J., and Saygin, Z. M. (2022). The language network is selective and distinct from other cognition in both function and connectivity in early childhood.

Hsu, N. S., Jaeggi, S. M., and Novick, J. M. (2017). A common neural hub resolves syntactic and non-syntactic conflict through cooperation with task-specific networks. *Brain and language*, 166:63–77.

Hu, J., Small, H., Kean, H., Takahashi, A., Zekelman, L., Kleinman, D., Ryan, E., Nieto-Castañón, A., Ferreira, V., and Fedorenko, E. (2023). Precision fMRI reveals that the language-selective network supports both phrase-structure building and lexical access during language production. *Cerebral Cortex*, 33(8):4384–4404.

Ibbotson, P. (2013). The scope of usage-based theory. *Frontiers in Psychology*, 4.

Indefrey, P., Brown, C. M., Hellwig, F., Amunts, K., Herzog, H., Seitz, R. J., and Hagoort, P. (2001). A neural correlate of syntactic encoding during speech production. *Proceedings of the National Academy of Sciences*, 98(10):5933–5936.

Indefrey, P., Hellwig, F., Herzog, H., Seitz, R. J., and Hagoort, P. (2004). Neural responses to the production and comprehension of syntax in identical utterances. *Brain and Language*, 89(2):312–319.

Ishkhanyan, B., Michel Lange, V., Boye, K., Mogensen, J., Karabanov, A., Hartwigsen, G., and Siebner, H. R. (2020). Anterior and posterior left inferior frontal gyrus contribute to the implementation of grammatical determiners during language production. *Frontiers in psychology*, 11:685.

Kemmerer, D. (2019). From blueprints to brain maps: the status of the lemma model in cognitive neuroscience. *Language, Cognition and Neuroscience*, 34(9):1085–1116.

Kleist, K. (1914). Aphasie und geisteskrankheit. *Münchener Medizinische Wochenschrift*, 61:8–12.

Kolk, H. and Heeschen, C. (1992). Agrammatism, paragrammatism and the management of language. *Language and cognitive processes*, 7(2):89–129.

Krauska, A. and Lau, E. (2023). Moving away from lexicalism in psycho- and neurolinguistics. *Frontiers in Language Sciences*, 2.

Krieger-Redwood, K. and Jefferies, E. (2014). TMS interferes with lexical-semantic retrieval

in left inferior frontal gyrus and posterior middle temporal gyrus: Evidence from cyclical picture naming. *Neuropsychologia*, 64:24–32.

Kyriaki, L., Todd, G., Schlesewsky, M., Devlin, J., and Bornkessel-Schlesewsky, I. (2020). Posterior superior temporal sulcus supports sequence-based language processing: Evidence from low-frequency repetitive transcranial magnetic stimulation.

LaCroix, A. N., James, E., and Rogalsky, C. (2021). Neural resources supporting language production vs. comprehension in chronic post-stroke aphasia: A meta-analysis using activation likelihood estimates. *Frontiers in Human Neuroscience*, 15.

Landrigan, J.-F., Zhang, F., and Mirman, D. (2021). A data-driven approach to post-stroke aphasia classification and lesion-based prediction. *Brain*, 144(5):1372–1383.

Le Normand, M.-T. and Thai-Van, H. (2022). The role of function words to build syntactic knowledge in French-speaking children. *Scientific reports*, 12(1):1–15.

Lee, D. K., Fedorenko, E., Simon, M. V., Curry, W. T., Nahed, B. V., Cahill, D. P., and Williams, Z. M. (2018). Neural encoding and production of functional morphemes in the posterior temporal lobe. *Nature communications*, 9(1):1–12.

Levelt, W. (1999). Producing spoken language. *The neurocognition of language*, pages 83–122.

Levelt, W. J., Roelofs, A., and Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and brain sciences*, 22(1):1–38.

Levelt, W. J. M. (1989). *Speaking: From Intention to Articulation*. The MIT Press.

Linebarger, M. C., Schwartz, M. F., and Saffran, E. M. (1983). Sensitivity to grammatical structure in so-called agrammatic aphasics. *Cognition*, 13(3):361–392.

Lipkin, B., Tuckute, G., Affourtit, J., Small, H., Mineroff, Z., Kean, H., Jouravlev, O., Rakocevic, L., Pritchett, B., Siegelman, M., et al. (2022). Probabilistic atlas for the language network based on precision fmri data from > 800 individuals. *Scientific data*, 9(1):1–10.

Lorca-Puls, D. L., Gajardo-Vidal, A., Mandelli, M. L., Illán-Gala, I., Ezzes, Z., Wauters, L. D., Battistella, G., Bogley, R., Ratnasiri, B., Licata, A. E., Battista, P., García, A. M., Tee, B. L., Lukic, S., Boxer, A. L., Rosen, H. J., Seeley, W. W., Grinberg, L. T., Spina, S., Miller, B. L., Miller, Z. A., Henry, M. L., Dronkers, N. F., and Gorno-Tempini, M. L. (2024). Neural basis of speech and grammar symptoms in non-fluent variant primary progressive aphasia spectrum. *Brain*.

Lukic, S., Thompson, C. K., Barbieri, E., Chiappetta, B., Bonakdarpour, B., Kiran, S., Rapp, B., Parrish, T. B., and Caplan, D. (2021). Common and distinct neural substrates of sentence production and comprehension. *NeuroImage*, 224:117374.

Maher, L., Rothi, L., and Heilman, K. (1994). Lack of error awareness in an aphasic patient with relatively preserved auditory comprehension. *Brain and Language*, 46(3):402–418.

Malyutina, S. and den Ouden, D.-B. (2017). Task-dependent neural and behavioral effects of verb argument structure features. *Brain and language*, 168:57–72.

Mandelli, M. L., Vilaplana, E., Brown, J. A., Hubbard, H. I., Binney, R. J., Attygalle, S., Santos-Santos, M. A., Miller, Z. A., Pakvasa, M., Henry, M. L., Rosen, H. J., Henry, R. G., Rabinovici, G. D., Miller, B. L., Seeley, W. W., and Gorno-Tempini, M. L. (2016). Healthy brain connectivity predicts atrophy progression in non-fluent variant of primary progressive aphasia. *Brain*, 139(10):2778–2791.

Marr, D. (1982). *Vision: A computational in-*

vestigation into the human representation and processing of visual information. MIT press.

Marshall, J. C. and Newcombe, F. (1988). Parasyndromes and paragrammatism. *Aphasiology*, 2(3-4):337–341.

Marshall, R. C. and Tompkins, C. A. (1982). Verbal self-correction behaviors of fluent and nonfluent aphasic subjects. *Brain and Language*, 15(2):292–306.

Matchin, W. (2023). Lexico-semantics obscures lexical syntax. *Frontiers in Language Sciences*, 2.

Matchin, W., Basilakos, A., Den Ouden, D.-B., Stark, B. C., Hickok, G., and Fridriksson, J. (2022a). Functional differentiation in the language network revealed by lesion-symptom mapping. *NeuroImage*, 247:118778.

Matchin, W., Basilakos, A., Stark, B. C., den Ouden, D.-B., Fridriksson, J., and Hickok, G. (2020). Agrammatism and paragrammatism: A cortical double dissociation revealed by lesion-symptom mapping. *Neurobiology of Language*, 1(2):208–225.

Matchin, W., den Ouden, D.-B., Basilakos, A., Stark, B. C., Fridriksson, J., and Hickok, G. (2023). Grammatical parallelism in aphasia: a lesion-symptom mapping study. *Neurobiology of Language*, pages 1–66.

Matchin, W., den Ouden, D. B., Hickok, G., Hillis, A. E., Bonilha, L., and Fridriksson, J. (2022b). The Wernicke conundrum revisited: Evidence from connectome-based lesion-symptom mapping. *Brain*, 06:awac219.

Matchin, W. and Hickok, G. (2020). The cortical organization of syntax. *Cerebral Cortex*, 30(3):1481–1498.

Matchin, W. and Wood, E. (2020). Syntax-sensitive regions of the posterior inferior frontal gyrus and the posterior temporal lobe are differentially recruited by production and perception. *Cerebral cortex communications*, 1(1):tgaa029.

Matias-Guiu, J. A., Díaz-Álvarez, J., Cuetos, F., Cabrera-Martín, M. N., Segovia-Ríos, I., Pytel, V., Moreno-Ramos, T., Carreras, J. L., Matías-Guiu, J., and Ayala, J. L. (2019). Machine learning in the clinical and language characterisation of primary progressive aphasia variants. *Cortex*, 119:312–323.

Menenti, L., Gierhan, S. M., Segaert, K., and Hagoort, P. (2011). Shared language: overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional MRI. *Psychological science*, 22(9):1173–1182.

Menenti, L., Segaert, K., and Hagoort, P. (2012). The neuronal infrastructure of speaking. *Brain and Language*, 122(2):71–80.

Mesulam, M.-M., Thompson, C. K., Weintraub, S., and Rogalski, E. J. (2015). The Wernicke conundrum and the anatomy of language comprehension in primary progressive aphasia. *Brain*, 138(8):2423–2437.

Miceli, G., Mazzucchi, A., Menn, L., and Goodglass, H. (1983). Contrasting cases of italian agrammatic aphasia without comprehension disorder. *Brain and language*, 19(1):65–97.

Miller, G. A. (1965). Some preliminaries to psycholinguistics. *American Psychologist*, 20(1):15–20.

Miller, G. A. and Chomsky, N. (1963). Finitary models of language users. In Luce, D., editor, *Handbook of Mathematical Psychology*, pages 2–419. John Wiley & Sons.

Mollica, F., Siegelman, M., Diachek, E., Piantadosi, S. T., Mineroff, Z., Futrell, R., Kean, H., Qian, P., and Fedorenko, E. (2020). Composition is the core driver of the language-selective network. *Neurobiology of Language*, 1(1):104–134.

Momma, S. and Phillips, C. (2018). The relationship between parsing and generation. *Annual Review of Linguistics*, 4(1):233–254.

Moreno, A., Limousin, F., Dehaene, S., and Pallier, C. (2018). Brain correlates of constituent structure in sign language comprehension. *NeuroImage*, 167:151–161.

Morgan, A. M., Devinsky, O., Doyle, W. K., Dugan, P., Friedman, D., and Flinker, A. (2024a). From single words to sentence production: Shared cortical representations but distinct temporal dynamics.

Morgan, A. M., Devinsky, O., Doyle, W. K., Dugan, P., Friedman, D., and Flinker, A. (2024b). A low-activity cortical network selectively encodes syntax.

Murphy, E. (2024a). Rose: A neurocomputational architecture for syntax. *Journal of Neurolinguistics*, 70:101180.

Murphy, E. (2024b). What is a word?

Murphy, E., Hoshi, K., and Benítez-Burraco, A. (2022). Subcortical syntax: Reconsidering the neural dynamics of language. *Journal of Neurolinguistics*, 62:101062.

Murphy, E., Rollo, P. S., Segaert, K., Hagoort, P., and Tandon, N. (2024). Multiple dimensions of syntactic structure are resolved earliest in posterior temporal cortex. *Progress in Neurobiology*, page 102669.

Murphy, E. and Woolnough, O. (2024). The language network is topographically diverse and driven by rapid syntactic inferences. *Nature Reviews Neuroscience*.

Nasios, G., Dardiotis, E., and Messinis, L. (2019). From Broca and Wernicke to the neuromodulation era: insights of brain language networks for neurorehabilitation. *Behavioural neurology*, 2019.

Novick, J. M., Trueswell, J. C., and Thompson-Schill, S. L. (2010). Broca's area and language processing: Evidence for the cognitive control connection. *Language and Linguistics Compass*, 4(10):906–924.

Ntemou, E., Svaldi, C., Jonkers, R., Picht, T., and Rofes, A. (2023). Verb and sentence processing with TMS: A systematic review and meta-analysis. *Cortex*, 162:38–55.

Papitto, G., Friederici, A. D., and Zaccarella, E. (2020). The topographical organization of motor processing: An ALE meta-analysis on six action domains and the relevance of Broca's region. *NeuroImage*, 206:116321.

Petersson, K. M. and Hagoort, P. (2012). The neurobiology of syntax: Beyond string sets. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1598):1971–1983.

Pickering, M. J. and Garrod, S. (2013). An integrated theory of language production and comprehension. *Behavioral and Brain Sciences*, 36(4):329–347.

Pietroski, P. M. (2018). *Conjoining Meanings: Semantics Without Truth Values*. Oxford University Press, Oxford, United Kingdom.

Poeppel, D. (2012). The maps problem and the mapping problem: Two challenges for a cognitive neuroscience of speech and language. *Cognitive Neuropsychology*, 29(1–2):34–55.

Poeppel, D. and Idsardi, W. (2022). We don't know how the brain stores anything, let alone words. *Trends in Cognitive Sciences*.

Price, A. R., Bonner, M. F., Peelle, J. E., and Grossman, M. (2015). Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *Journal of Neuroscience*, 35(7):3276–3284.

Pylkkänen, L. (2016). Composition of complex meaning: Interdisciplinary perspectives on the

left anterior temporal lobe. In *Neurobiology of language*, pages 621–631. Elsevier.

Pylkkänen, L. (2019). The neural basis of combinatory syntax and semantics. *Science*, 366(6461):62–66.

Pylkkänen, L. (2020). Neural basis of basic composition: what we have learned from the red–boat studies and their extensions. *Philosophical Transactions of the Royal Society B*, 375(1791):20190299.

Pylkkänen, L. and Brennan, J. R. (2020). *The Neurobiology of Syntactic and Semantic Structure Building*, page 859–868. The MIT Press.

Qu, X., Wang, Z., Cheng, Y., Xue, Q., Li, Z., Li, L., Feng, L., Hartwigsen, G., and Chen, L. (2022). Neuromodulatory effects of transcranial magnetic stimulation on language performance in healthy participants: Systematic review and meta-analysis. *Frontiers in Human Neuroscience*, 16.

Quillen, I. A., Yen, M., and Wilson, S. M. (2021). Distinct neural correlates of linguistic and non-linguistic demand. *Neurobiology of Language*, 2(2):202–225.

Rajkumar, R., van Schijndel, M., White, M., and Schuler, W. (2016). Investigating locality effects and surprisal in written english syntactic choice phenomena. *Cognition*, 155:204–232.

Razafimahatratra, S., Guieysse, T., Lejeune, F.-X., Houot, M., Medani, T., Dreyfus, G., Klarsfeld, A., Villain, N., Pereira, F. R., La Corte, V., George, N., Pantazis, D., and Andrade, K. (2023). Can a failure in the error-monitoring system explain unawareness of memory deficits in alzheimer's disease? *Cortex*, 166:428–440.

Rezaii, N., Mahowald, K., Ryskin, R., Dickerson, B., and Gibson, E. (2022). A syntax–lexicon trade-off in language production. *Proceedings of the National Academy of Sciences*, 119(25):e2120203119.

Rezaii, N., Ren, B., Quimby, M., Hochberg, D., and Dickerson, B. C. (2023). Less is more in language production: an information-theoretic analysis of agrammatism in primary progressive aphasia. *Brain Communications*.

Riva, M., Wilson, S. M., Cai, R., Castellano, A., Jordan, K. M., Henry, R. G., Gorno-Tempini, M. L., Berger, M. S., and Chang, E. F. (2023). Evaluating syntactic comprehension during awake intraoperative cortical stimulation mapping. *Journal of Neurosurgery*, 1(aop):1–8.

Rodd, J. M., Vitello, S., Woollams, A. M., and Adank, P. (2015). Localising semantic and syntactic processing in spoken and written language comprehension: An activation likelihood estimation meta-analysis. *Brain and Language*, 141:89–102.

Roelofs, A. (2022). A neurocognitive computational account of word production, comprehension, and repetition in primary progressive aphasia. *Brain and Language*, 227:105094.

Roelofs, A. and Ferreira, V. S. (2019). *The Architecture of Speaking*, page 35–50. The MIT Press.

Rogalsky, C., Almeida, D., Sprouse, J., and Hickok, G. (2015). Sentence processing selectivity in Broca's area: Evident for structure but not syntactic movement. *Language, cognition and neuroscience*, 30(10):1326–1338.

Rogalsky, C., LaCroix, A. N., Chen, K.-H., Anderson, S. W., Damasio, H., Love, T., and Hickok, G. (2018). The neurobiology of agrammatic sentence comprehension: A lesion study. *Journal of Cognitive Neuroscience*, 30(2):234–255.

Rogalsky, C., Matchin, W., and Hickok, G. (2008). Broca's area, sentence comprehension, and working memory: an fMRI study. *Frontiers in human neuroscience*, 2:14.

Sahin, N. T., Pinker, S., Cash, S. S., Schomer, D., and Halgren, E. (2009). Sequential processing of lexical, grammatical, and phonological information within Broca's area. *Science*, 326(5951):445–449.

Sahraoui, H. and Nespoulous, J.-L. (2012). Across-task variability in agrammatic performance. *Aphasiology*, 26(6):785–810.

Salis, C. and Edwards, S. (2004). Adaptation theory and non-fluent aphasia in english. *Aphasiology*, 18(12):1103–1120.

Schell, M., Zaccarella, E., and Friederici, A. D. (2017). Differential cortical contribution of syntax and semantics: An fMRI study on two-word phrasal processing. *Cortex*, 96:105–120.

Schönberger, E., Heim, S., Meffert, E., Pieperhoff, P., da Costa Avelar, P., Huber, W., Binkofski, F., and Grande, M. (2014). The neural correlates of agrammatism: Evidence from aphasic and healthy speakers performing an overt picture description task. *Frontiers in Psychology*, 5.

Segaert, K., Menenti, L., Weber, K., Petersson, K. M., and Hagoort, P. (2012). Shared syntax in language production and language comprehension—an fMRI study. *Cerebral Cortex*, 22(7):1662–1670.

Shain, C., Blank, I. A., Fedorenko, E., Gibson, E., and Schuler, W. (2022). Robust effects of working memory demand during naturalistic language comprehension in language-selective cortex. *Journal of Neuroscience*.

Shain, C., Kean, H., Casto, C., Lipkin, B., Affourtit, J., Siegelman, M., Mollica, F., and Fedorenko, E. (2024). Distributed sensitivity to syntax and semantics throughout the language network. *Journal of Cognitive Neuroscience*, page 1–43.

Sheng, J., Zheng, L., Lyu, B., Cen, Z., Qin, L., Tan, L. H., Huang, M.-X., Ding, N., and Gao, J.-H. (2019). The cortical maps of hierarchical linguistic structures during speech perception. *Cerebral cortex*, 29(8):3232–3240.

Siegelman, M., Blank, I. A., Mineroff, Z., and Fedorenko, E. (2019). An attempt to conceptually replicate the dissociation between syntax and semantics during sentence comprehension. *Neuroscience*, 413:219–229.

Skeide, M. A., Brauer, J., and Friederici, A. D. (2014). Syntax gradually segregates from semantics in the developing brain. *Neuroimage*, 100:106–111.

Skeide, M. A., Brauer, J., and Friederici, A. D. (2016). Brain functional and structural predictors of language performance. *Cerebral Cortex*, 26(5):2127–2139.

Skinner, B. F. (1957). *Verbal behavior*. Appleton-Century-Crofts.

Snell, J. and Grainger, J. (2017). The sentence superiority effect revisited. *Cognition*, 168:217–221.

Stark, B. C., Basilakos, A., Hickok, G., Rorden, C., Bonilha, L., and Fridriksson, J. (2019). Neural organization of speech production: A lesion-based study of error patterns in connected speech. *Cortex*, 117:228–246.

Steels, L. and De Beule, J. (2006). *Unify and Merge in Fluid Construction Grammar*, page 197–223. Springer Berlin Heidelberg.

Takashima, A., Konopka, A., Meyer, A., Hagoort, P., and Weber, K. (2020). Speaking in the brain: the interaction between words and syntax in sentence production. *Journal of Cognitive Neuroscience*, 32(8):1466–1483.

Thompson, C. K., Faroqi-Shah, Y., and Lee, J. (2015). Models of sentence production. In *The handbook of adult language disorders*, pages 328–354. Psychology Press.

Tourville, J. A. and Guenther, F. H. (2011). The diva model: A neural theory of speech acquisition and production. *Language and cognitive processes*, 26(7):952–981.

Tremblay, P. and Dick, A. S. (2016). Broca and Wernicke are dead, or moving past the classic model of language neurobiology. *Brain and language*, 162:60–71.

Turken, A. and Dronkers, N. F. (2011). The neural architecture of the language comprehension network: Converging evidence from lesion and connectivity analyses. *Frontiers in System Neuroscience*, 5:1.

Turker, S., Kuhnke, P., Eickhoff, S. B., Caspers, S., and Hartwigsen, G. (2023). Cortical, subcortical, and cerebellar contributions to language processing: A meta-analytic review of 403 neuroimaging experiments. *Psychological Bulletin*, 149(11–12):699–723.

Uddén, J., Hultén, A., Schoffelen, J.-M., Harbusch, K., van den Bosch, A., Kempen, G., Petersson, K. M., and Hagoort, P. (2022). Supramodal sentence processing in the human brain: fmri evidence for the influence of syntactic complexity in more than 200 participants. *Neurobiology of Language*, 3(4):575–598.

Uddén, J. and Männel, C. (2018). Artificial grammar learning and its neurobiology in relation to language processing and development. In *The Oxford Handbook of Psycholinguistics*, pages 755–783. Oxford University Press.

Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., and Pinker, S. (1997). A neural dissociation within language: Evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *Journal of cognitive neuroscience*, 9(2):266–276.

Vissiennon, K., Friederici, A. D., Brauer, J., and Wu, C.-Y. (2017). Functional organization of the language network in three- and six-year-old children. *Neuropsychologia*, 98:24–33.

Walenski, M., Europa, E., Caplan, D., and Thompson, C. K. (2019). Neural networks for sentence comprehension and production: An ALE-based meta-analysis of neuroimaging studies. *Human brain mapping*, 40(8):2275–2304.

Wang, H., Yoshida, M., and Thompson, C. K. (2014). Parallel functional category deficits in clauses and nominal phrases: The case of English agrammatism. *Journal of Neurolinguistics*, 27(1):75–102.

Weber, K., Meyer, A., and Hagoort, P. (2019). Learning lexical-syntactic biases: An fMRI study on how we connect words and syntactic information. bioRxiv.

Wernicke, C. (1874). *The symptom complex of aphasia. A psychological study on an anatomical basis (Translated from German)*. Springer.

Whitwell, J. L., Duffy, J. R., Machulda, M. M., Clark, H. M., Strand, E. A., Senjem, M. L., Gunter, J. L., Spychalla, A. J., Petersen, R. C., Jack Jr, C. R., et al. (2017). Tracking the development of agrammatic aphasia: A tensor-based morphometry study. *Cortex*, 90:138–148.

Williams, A., Reddigari, S., and Pylkkänen, L. (2017). Early sensitivity of left perisylvian cortex to relationality in nouns and verbs. *Neuropsychologia*, 100:131–143.

Wilson, S. M., Brandt, T. H., Henry, M. L., Babiak, M., Ogar, J. M., Salli, C., Wilson, L., Peralta, K., Miller, B. L., and Gorno-Tempini, M. L. (2014a). Inflectional morphology in primary progressive aphasia: An elicited production study. *Brain and language*, 136:58–68.

Wilson, S. M., DeMarco, A. T., Henry, M. L., Gesierich, B., Babiak, M., Mandelli, M. L., Miller, B. L., and Gorno-Tempini, M. L.

(2014b). What role does the anterior temporal lobe play in sentence-level processing? Neural correlates of syntactic processing in semantic variant primary progressive aphasia. *Journal of Cognitive Neuroscience*, 26(5):970–985.

Wilson, S. M., Galantucci, S., Tartaglia, M. C., Rising, K., Patterson, D. K., Henry, M. L., Ogar, J. M., DeLeon, J., Miller, B. L., and Gorno-Tempini, M. L. (2011). Syntactic processing depends on dorsal language tracts. *Neuron*, 72(2):397–403.

Wilson, S. M., Henry, M. L., Besbris, M., Ogar, J. M., Dronkers, N. F., Jarrold, W., Miller, B. L., and Gorno-Tempini, M. L. (2010). Connected speech production in three variants of primary progressive aphasia. *Brain*, 133(7):2069–2088.

Xiang, H.-D., Fonteijn, H. M., Norris, D. G., and Hagoort, P. (2010). Topographical functional connectivity pattern in the perisylvian language networks. *Cerebral cortex*, 20(3):549–560.

Yagata, S. A., Yen, M., McCarron, A., Bautista, A., Lamair-Orosco, G., and Wilson, S. M. (2017). Rapid recovery from aphasia after infarction of Wernicke's area. *Aphasiology*, 31(8):951–980.

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., and Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature methods*, 8(8):665–670.

Yeaton, J. (2022). A review of the neurobiology of syntax. Unpublished Master's thesis.

Yeaton, J., Fahey, D., Khosshal Mollasaraei, Z., Krauska, A., and Matchin, W. (2025). Aligning psycholinguistics, neuroscience, and aphasiology with respect to grammatical encoding. PsyArXiv.

Yeaton, J., Fahey, D., Stark, B., and Matchin, W. (2024). Neural correlates of

(par)agrammatic production in post-stroke aphasia. Manuscript in preparation.

Yeaton, J., Fahey, D., Stark, B., Matchin, W., and Hickok, G. (2023). Evidence for a syntactic production-comprehension asymmetry in post-stroke aphasia. Manuscript in preparation.

Zaccarella, E. and Friederici, A. D. (2015). Merge in the human brain: A sub-region based functional investigation in the left pars opercularis. *Frontiers in psychology*, 6:1818.

Zaccarella, E., Meyer, L., Makuuchi, M., and Friederici, A. D. (2017). Building by syntax: The neural basis of minimal linguistic structures. *Cerebral Cortex*, 27(1):411–421.

Zilles, K. and Amunts, K. (2018). Cytoarchitectonic and receptorarchitectonic organization in broca's region and surrounding cortex. *Current opinion in behavioral sciences*, 21:93–105.

Zyryanov, A., Malyutina, S., and Dragoy, O. (2020). Left frontal aslant tract and lexical selection: Evidence from frontal lobe lesions. *Neuropsychologia*, 147:107385.