Grammatical Parallelism in Aphasia Revisited

William Matchin, Alexandra Basilakos, Brielle Stark,
Dirk-Bart den Ouden, Julius Fridriksson and Gregory Hickok

September 7, 2021

Abstract

Syntactic production and comprehension deficits in aphasia, both of which are commonly referred to as "agrammatism", are commonly thought to result from a common underlying grammatical deficit, associated with frontal lesions centered on Broca's area. However, Wernicke originally posited that frontal damage resulted in nonfluent speech production but not comprehension deficits, and that parallel production and comprehension deficits in fluent aphasia result from damage to posterior temporal cortex. In this study we tested the generalization of Wernicke's theory to syntax. In a group of 53 left hemisphere stroke patients, paragrammatic production deficits were associated with reliable syntactic comprehension deficits, but agrammatic production deficits were not. In addition, the lesion corelates of syntactic comprehension deficits in 218 left hemisphere stroke patients were associated with damage to the same temporal lobe regions implicated in paragrammatism, but not the inferior and middle frontal regions implicated in agrammatism. Our results speak against the received view of parallel syntactic production and comprehension deficits resulting from common damage to frontal cortex. By contrast, consistent with Wernicke's original ideas, a different grammatical parallelism hypothesis appears to be correct: syntactic production and comprehension deficits occur in fluent aphasia following damage to middle and posterior temporal lobe.

Significance statement

Sentence structure, or syntax, is potentially a uniquely creative aspect of the human mind, widely thought to be associated with Broca's area in the frontal lobe. This association was forged after experiments in the 1970s with few subjects suggested parallel syntactic production and comprehension deficits in Broca's aphasia. Using modern lesion-symptom mapping methods in large numbers of subjects, we found that, contrary to the standard view, parallel syntactic production and comprehension deficits result from damage to the middle-posterior temporal lobe and not the frontal lobe. Our results suggest a fundamental rethinking of the neurological bases of this creative capacity, in line with older hypotheses about parallel production and comprehension deficits developed in the 19th century by Karl Wernicke.

Introduction

Grammatical parallelism in aphasia

Syntax, or the ability to combine words into hierarchical structures, enables a core component of human linguistic creativity: the ability to make novel sentences of unbounded size and number (Chomsky, 1965; von Humboldt, 1836). The nature of syntactic deficits in aphasia and the role of Broca's area in such deficits has a long and complicated history. From the beginning of the 20th century until the 1970s, agrammatism in people with nonfluent Broca's aphasia was defined as the systematic reduction of syntactic complexity and omission of functional elements (such as auxiliary verbs and articles) in speech production; syntactic comprehension was assumed to be intact (Forster, 1919; Isserlin, 1922). This was consistent with the classical model of language in the brain espoused by Wernicke, Lichtheim, and later Geschwind, positing that frontal damage, which was linked to Broca's aphasia, produced expressive language deficits in the absence of notable receptive deficits (Geschwind, 1970, 1972, 1979; Wernicke, 1874).

The received view of impaired production but preserved comprehension in agrammatism was questioned in the 1970s, when some studies (typically with small numbers of subjects and an absence of detailed lesion analysis) revealed apparent syntactic comprehension deficits in people with agrammatic Broca's aphasia (Caramazza & Zurif, 1976; Zurif et al., 1972)[1]. A highly influential study by Caramazza & Zurif (1976) assessed the syntactic comprehension abilities of English speaking people with agrammatic Broca's aphasia using semantically reversible sentences with noncanonical word order. Reversible sentences consisted of those in which the doer and receiver of the action could switch positions and the sentence still makes sense (1), as opposed to semantically constrained sentences which would be thematically impossible if the doer and receiver were switched (2).

(1) The man that the woman is hugging is happy (reversible, non-canonical word order, **poor performance**)
(2) The apple that the boy is eating is red (semantically constrained, non-canonical word order, **good performance**)

This study showed that comprehension of semantically constrained sentences with non-canonical word order (2) was good, but that comprehension of reversible sentences with non-canonical word order (1) was poor. They argued that people with agrammatic Broca's aphasia lacked normal syntactic ability not only for production but also comprehension, explaining their selective pattern of comprehension deficits. This pattern could be explained via the preservation of word-level understanding and interpretive heuristics based on semantic plausibility and assuming the first noun to be the agent of the action.

Such results shifted the standard assumption in aphasiology towards grammatical parallelism: the idea that syntactic comprehension deficits accompanied syntactic production deficits in agrammatic Broca's aphasia (Berndt & Caramazza, 1980; Kean, 1977; Saffran et al., 1980; Schwartz et al., 1980; Zurif, 1980). The grammatical parallelism hypothesis was sometimes termed "overarching agrammatism" (Swinney & Zurif, 1995; Grodzinsky, 2000), emphasizing that the comprehension and production deficits in agrammatism resulted from disruption to a common underlying syntactic mechanism. This represented a major shift in thinking regarding aphasiology and the neurobiology of language. Instead of talking about language deficits and neurological models in terms of production or comprehension functions, the vocabulary of linguistic theory regarding central functions of syntax (assumed to be Broca's area, or the posterior inferior frontal gyrus) and semantics (assumed to be posterior temporal cortex) was used to define the language-brain relationship (see also Jakobson, 1956; Jakobson & Halle, 1956 for early views on the application of linguistics to aphasiology). This was in part based on the assumed relationship between Broca's aphasia and Broca's area, although we note that Broca's aphasia may be caused by lesions not involving Broca's area (Fridriksson et al., 2007), and damage to Broca's area alone is insufficient to cause Broca's aphasia (Fridriksson et al., 2015; Mohr et al., 1978).

[1] Patients with conduction aphasia, without agrammatic production deficits, showed the same comprehension pattern in Caramazza & Zurif (1976), a fact rarely discussed in current literature.

However, demonstrations of intact receptive syntactic abilities in people with agrammatic Broca's aphasia in the 1980s cast strong doubt on the grammatical parallelism hypothesis. Specifically, syntactic acceptability judgments, subtle and direct tests of syntactic ability, were shown to be intact in people with agrammatic Broca's aphasia (Linebarger et al., 1983; Wilson & Saygın, 2004; Wulfeck & Bates, 1991). Thus by the 1990s, researchers in aphasiology had largely abandoned the grammatical parallelism hypothesis (Goodglass et al., 1993; Kean, 1995; Swinney & Zurif, 1995) for a review, see (Matchin & Rogalsky, in press).

The idea that Broca's area serves as a central syntactic hub may have disappeared completely from the theoretical landscape had it not been for the emergence of functional neuroimaging studies of syntactic processing in the 1990s. Several studies of syntactic comprehension showed effects in Broca's area (Dapretto & Bookheimer, 1999; Embick et al., 2000; Friederici et al., 2000; Moro et al., 2001; Stromswold et al., 1996), breathing new life into the hypothesis that Broca's area serves as a overarching syntactic hub. In addition, research on the neural basis of word-level processes (lexical access) demonstrated associations with the posterior temporal lobe (Dronkers et al., 2004; Hickok & Poeppel, 2000; Lau et al., 2008; Levelt, 2001; Levelt et al., 1999; Pinker & Ullman, 2002). Together, these findings reinforced a framework for language in the brain that posited a syntactic computation function in Broca's area and a lexical storage function in posterior temporal cortex (Friederici, 2002; Hagoort, 2005), aligning two core aspects of language with the two classical language regions. Thus, despite contradictory evidence from aphasiology, the overarching agrammatism hypothesis and the concept of a central syntactic hub in Broca's area continues to have substantial influence in psychology, linguistics, and neuroscience (Arbib, 2016; Bozic et al., 2015; Friederici, 2017; Hagoort, 2013, 2016; Hagoort & Indefrey, 2014; Kuperberg, 2007; Menenti et al., 2011; Momma & Phillips, 2018; Rilling, 2014; Tyler et al., 2010; Wilson et al., 2010)(D'Ausilio et al., 2012; Ocampo & Kritikos, 2011; Pulvermüller & Fadiga, 2010).

Grammatical parallelism revisited: paragrammatism and the posterior temporal lobe

Juxtaposed with the idea that Broca's area is a hub for an overarching grammatical ability is the emerging view that there is a kind of overarching syntactic hub in the posterior temporal lobe instead. Roots of this idea extend back to Wernicke (1874) who argued that the temporal lobe subserved both receptive and expressive function at the speech-sound level. Specifically, he observed that people with sensory (Wernicke's) aphasia had production deficits in addition to comprehension deficits, which he attributed to the absence of a sensory-to-motor "corrective function."

> *Aside from his deficient comprehension, the patient has aphasic manifestations in speaking because of the absence of the corrective function exercised unconsciously by the sound images*. (p. 52)

In today's terminology, we would call this "sensory feedback control": the idea that production is guided by perceptual systems (Guenther, 2006; Guenther & Hickok, 2016; Levelt, 1989). Much subsequent research has confirmed the role of posterior temporal regions in phonological- and lexical-level aspects of speech production (Behroozmand et al., 2015; DeLeon et al., 2007;

Dell et al., 2013; Golfinopoulos et al., 2011; Guenther & Hickok, 2015; Hickok, 2012, 2014b; Hickok et al., 2003, 2011; Hillis et al., 2006; Indefrey & Levelt, 2004; Tourville et al., 2008).

Expressive deficits in such people with aphasia are not limited to sound-related errors, however. In the early 1900s, clinicians described an expressive disorder termed *paragrammatism*, which is associated with fluent aphasia and characterized by grammatical distortion but without the overall reduction/simplification that is characteristic of agrammatism (Bonhoeffer, 1902; Butterworth & Howard, 1987; Goodglass et al., 1993; Kleist, 1914). This disorder has received vanishingly little attention in the last decades. In recent work, Matchin et al. (2020) found a double dissociation in the lesion distributions associated with agrammatism versus paragrammatism: agrammatism was associated with inferior and middle frontal damage including Broca's area, but not temporal cortex, consistent with several previous studies (Den Ouden et al., 2019; Sapolsky et al., 2010; Wilson et al., 2011; Wilson, Henry, et al., 2010), and paragrammatism was associated with damage to the posterior temporal cortex, but not frontal cortex.

The finding of expressive grammatical deficits associated with posterior temporal lesions strongly suggests the existence of an overarching grammatical deficit for three reasons. First, paragrammatism is strongly associated with the fluent aphasias (Wernicke's and conduction aphasia) and poor comprehension (Butterworth & Howard, 1987; Goodglass et al., 1993; Heeschen, 1985; Yagata et al., 2017), which are associated with posterior temporal-parietal rather than frontal lesions (Buchsbaum et al., 2011; Fridriksson et al., 2018; Hillis et al., 2001; Ogar et al., 2011; Yagata et al., 2017). Second, posterior temporal regions have consistently been implicated in both lesion and functional imaging studies of syntactic comprehension (Fedorenko et al., 2012; Goucha & Friederici, 2015; Matchin, Brodbeck, et al., 2019; Matchin et al., 2017; Matchin, Liao, et al., 2019; Matchin & Wood, 2020; Pallier et al., 2011; Rogalsky et al., 2018; Wilson & Saygın, 2004; Zaccarella, Meyer, et al., 2017). By contrast, frontal cortex is not consistently implicated in lesion studies of receptive syntax and when it is, the sentence stimuli used in such studies carry steep working memory demands, such as complex multi-clause structures with non-canonical word order (Amici et al., 2007; Fridriksson et al., 2018; Kristinsson et al., 2020; Magnusdottir et al., 2013; Mesulam et al., 2015; Tyler et al., 2011; Wilson et al., 2011). Third, the concept of lexicalized syntactic structure—the idea that syntax is stored in the lexicon—has emerged as a strong convergent idea across linguistic theories (see Matchin & Hickok, 2020 for an overview). Thus, posterior temporal regions are a much stronger candidate for an overarching grammatical function than frontal areas.

Here we test the overarching paragrammatism hypothesis directly in a large sample of people with aphasia. We assess whether syntactic production and comprehension deficits coincide in aphasia, and whether damage to frontal or posterior temporal regions result in parallel grammatical deficits. As reviewed above, syntactic comprehension is often assessed using reversible sentences with non-canonical word order, but such structures typically involve complex multi-clause structures with working memory confounds (Rogalsky et al., 2008). Therefore, for our measure of syntactic comprehension, we instead used the Sequential Commands subtest of the Western Aphasia Battery/Western Aphasia Battery-Revised (WAB/WAB-R; Kertesz, 2007), which we administered to a large cohort of 218 subjects. Sequential Commands consists of 11 sentential instructions for simple actions to perform. It requires the subject to process basic syntactic relations indicated with prepositional phrase modifiers and connectives, while minimizing lexical demands (using repeated simple nouns referring to objects in the room) and minimizing the working memory demands that complex non-canonical structures involve[2]. Previous studies have also used the Sequential Commands subtest of the WAB to assess syntactic comprehension (Dronkers et al., 2004; Gorno-Tempini et al., 2004), but did so in conjunction with additional measures including complex sentences with non-canonical word order. We combined the Sequential Commands scores with performance on the Auditory Word Recognition subtest of the WAB-R to control for lexical comprehension abilities. The Auditory Word Recognition Subtest requires the subject to identify similar household objects as in the Sequential Commands subtest indicated by the experimenter in addition to a variety of other common words that are visually depicted. We included Auditory Word Recognition scores as a covariate on the Sequential Commands scores, removing the variance associated with word comprehension, resulting in our syntactic comprehension measure.

For our measures of syntactic production deficits, we use the same data from 53 subjects reported in (Matchin et al., 2020): expert assessments of the presence and type of grammatical production deficits (agrammatism, paragrammatism, and no grammatical deficit). We assessed the relationship between these grammatical production deficits, syntactic comprehension deficits, and their associated lesion correlates. The overarching paragrammatism hypothesis predicts that posterior temporal lobe lesions will be associated with syntactic comprehension deficits and with the presence of paragrammatic speech output. Although existing neuropsychological evidence argues against the idea of overarching *agrammatism* following frontal lesions, we will test the predictions of this hypothesis as well. The overarching agrammatism hypothesis predicts that frontal lesions will be associated with syntactic comprehension deficits and with the presence of agrammatic speech output.

Materials and Methods

Subjects

Subjects were drawn from a database of individuals with chronic, post-stroke aphasia who have completed testing for various studies conducted at the University of South Carolina (UofSC) and the Medical University of South Carolina (MUSC) over the last 15 years. All were right-handed, native speakers of English, had suffered an ischemic stroke to the left hemisphere at least six months prior to the study, and presented with language difficulties[3]. We performed analyses in two groups of subjects. The first group consisted of 218 subjects who were assessed on the Sequential Commands and Auditory Word Recognition subtests of the Auditory Verbal Comprehension section of the WAB/WAB-R. The second group consisted of a subset of 53 of

[2] A few items require the subject to perform actions in sequence, which might involve working memory demands. However, we note that this possibility works against our hypothesis, as it would suggest that frontal resources in addition to temporal resources would be additionally recruited to perform the task. Importantly, the sentence stimuli in Sequential Commands do not themselves impose a working memory burden in the way that complex non-canonical structures do, such as embedded object-relative clauses.

[3] Most subjects were classified as aphasic according to the Western Aphasia Battery; however, some scored outside of the aphasic range by the time of examination. All subjects had presented with some form of language difficulty following their stroke.

these subjects who also performed the Cinderella Story retelling task from AphasiaBank (MacWhinney et al., 2011), for which we were able to assess the presence of paragrammatic and agrammatic speech as reported in Matchin et al. (2020); detailed information about this group is reported in that paper. All procedures were approved by the UofSC and MUSC IRBs and informed consent was obtained.

Tasks	WAB/WAB-R: Sequential Commands and Auditory Word Recognition	Perceptual ratings: AGRAMMATISM and PARAGRAMMATISM
Total number of subjects	218	53
Sex	133 male, 85 female	35 male, 18 female
Mean age at testing (years)	60.0 (SD = 11.4)	58.9 (SD = 12.2)
Mean months post-stroke at initial testing	43.0 (SD = 48.4)	48.6 (SD = 53.5)
Mean education (years)	15.0 (SD = 2.3)*	15.8 (SD = 2.3)
Mean lesion volume (mm^3)	120,855 (SD = 97,488)	125,102 (SD = 85,490)
Mean WAB-R AQ	61.4 (SD = 28.1)	68.2 (SD = 16.7)

Table 1. Subject information for the two partially overlapping groups of subjects. SD = standard deviation. AQ = aphasia quotient of the Western Aphasia Batter-Revised, a summary measure of overall language ability. * education information was available for only 210/218 of these subjects.

Measures and Procedure

All 218 subjects were evaluated using the WAB or the WAB-R (Kertesz, 2007) to determine the presence and severity of aphasia. The test was administered and scored by certified speech-language pathologists with extensive experience evaluating individuals with aphasia. The WAB/WAB-R contains multiple subtests to evaluate production and comprehension ability; here we focus on the Sequential Commands and Auditory Word Recognition subtests.

The sentences contained within the Sequential Commands subtest are shown below. While sentences 1-3 (and arguably 5) can be performed correctly without syntactic analysis, relying on lexical comprehension alone, sentences 4 and 6-11 (shown in bold), which contribute the bulk of the total score (70/80 total points), require analyzing both the lexical items and their syntactic arrangement to perform correctly. Indeed, Schwartz et al. (1980) report that people with agrammatic Broca's aphasia have difficulty comprehending sentences of this type. Subjects can receive partial credit for correctly performing a subset of the actions indicated in a command; full credit required performing all of the indicated actions in the correct order.

1. Raise your hand. (2 points)
2. Shut your eyes. (2 points)

3. Point to the chair. (2 points)
4. **Point to the window, then to the door. (4 points)**
5. Point to the pen and the book. (4 points)
6. **Point with the pen to the book. (8 points)**
7. **Point to the pen with the book. (8 points)**
8. **Point to the comb with the pen. (8 points)**
9. **With the book point to the comb. (8 points)**
10. **Put the pen on top of the book then give it to me. (14 points)**
11. **Put the comb on the other side of the pen and turn over the book. (20 points)**

The Auditory Word Recognition subtest involves asking the subject to point to real-world objects or printed images as requested. Some of these objects are contained within the Sequential Commands subtest. Subjects are prompted with a sentence, e.g. "point to the __" or "show me the __". The test involves multiple types of tested words, including real household objects (cup, matches, pencil, flower, comb, screwdriver), pictured objects (the same as real objects), pictured shapes (square, triangle, circle, arrow, cross, cylinder), pictured letters (J, F, B, K, M, D), pictured numbers (5, 61, 500, 1867, 32, 5000), pictured colors (blue, brown, red, green, yellow, black), real world furniture (window, chair, desk or bed, light, door, ceiling), real world body parts (ear, nose, eye, chest, neck, chin), real world fingers (thumb, ring finger, index finger, little finger, middle finger), and real world body parts on the correct side (right ear, right shoulder, left knee, left ankle, right wrist, left elbow, right cheek). For each item the subject receives 1 point, for a total of 60 points.

To derive our SYNTACTIC COMPREHENSION measure, we performed a linear regression on Sequential Commands scores in SPSS using Auditory Word Recognition scores as a covariate, saving the residual scores. This removes variability due to simple word comprehension, leaving residual variance associated with comprehension of the sentence structure required to perform the commands correctly. Throughout the paper, we refer to SYNTACTIC COMPREHENSION in small capital typeface as this residual score, and syntactic comprehension in regular type as the general concept of the ability to comprehend syntax.

We used the same measures of AGRAMMATISM and PARAGRAMMATISM from Matchin et al. (2020): categorical perceptual ratings, formed as a consensus of four expert raters based on their unconstrained retelling of the Cinderella Story in their own words, following the AphasiaBank protocol (MacWhinney et al., 2011). Each subject was classified as AGRAMMATIC (11 subjects), PARAGRAMMATIC (21 subjects), no grammatical deficit (17 subjects), or both AGRAMMATIC and PARAGRAMMATIC (4 subjects). Following Kleist (1914), AGRAMMATIC patients were defined as those exhibiting an overall tendency to omit function words and morphemes, with reduced sentence complexity, whereas PARAGRAMMATIC patients were defined as those making grammatical errors not resulting from an overall pattern of reduction or omission of functional elements. Four patients were identified exhibiting some features of both classifications, and thus were included in analyses of both of these measures; thus we had a total of 15 AGRAMMATIC subjects and 25 PARAGRAMMATIC subjects. More detail about these patients and our inclusion criteria is reported in Matchin et al. (2020). Throughout the paper, we express the general concepts discussed in the literature of agrammatism (and agrammatic speech) and paragrammatism (and paragrammatic speech) using regular typeface. We express the corresponding perceptual classification of these concepts as applied to our subject groups using small capital typeface, that is, AGRAMMATISM/AGRAMMATIC and PARAGRAMMATISM/PARAGRAMMATIC.

Neuroimaging

We acquired anatomical MRIs and performed lesion mapping using the same parameters and procedures as described in Fridriksson et al. (2018) and Matchin et al. (2020). Neuroimaging data were collected at UofSC and the MUSC. Lesions were demarcated onto each subject's T2 image by an expert technician (Roger Newman-Norlund) or an expert neurologist (Leo Bonilha) blind to the behavioral data. The subject's T1 image was then warped to MNI space and the resulting transformation was applied to the lesion mask. A lesion overlap map for each of the groups included in these analyses is shown in Figure 1.

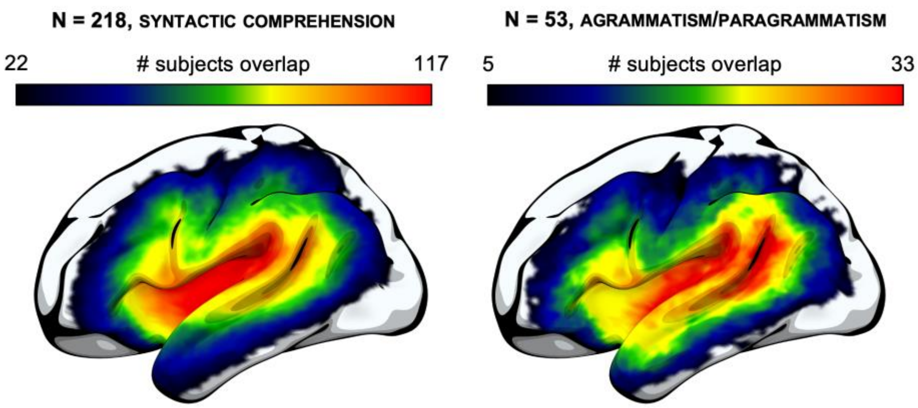

Figure 1. Lesion overlap maps for the two groups of subjects. The lower bound indicates the lower bound of the lesion load threshold, i.e. the minimum number of subjects with damage to a voxel required for statistical analysis. LEFT: the broader set of 218 subjects who were enrolled in all measures, including the SYNTACTIC COMPREHENSION measure. RIGHT: the subset of 53 subjects who were assessed for AGRAMMATISM and PARAGRAMMATISM.

Analyses

In our first pass of behavioral analyses, we simply assessed SYNTACTIC COMPREHENSION by comparing AGRAMMATIC and PARAGRAMMATIC subjects to their not AGRAMMATIC and not PARAGRAMMATIC counterparts using independent samples t-tests. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$.

In a second set of behavioral analyses, we incorporated lesion volume as a covariate to our categorical ratings of AGRAMMATISM and PARAGRAMMATISM and correlated these measures with the SYNTACTIC COMPREHENSION measure. The AGRAMMATIC subjects in our sample have nearly twice the lesion volume of the PARAGRAMMATIC subjects (Matchin et al., 2020), thus presenting potential confounds. The lesion volume differences are likely due to vasculature differences in these lesion distributions (DeMarco & Turkeltaub, 2018). In particular, we suspected that some of the AGRAMMATIC patients might have comprehension deficits because their (comparatively larger) frontal-based lesions encroach onto the temporal lobe, which is consistent with the fact that chronic Broca's aphasia reliably implicates posterior temporal as well as frontal damage (Fridriksson et al., 2015). By incorporating lesion volume as a covariate in our binary ratings of AGRAMMATISM and PARAGRAMMATISM, we controlled for these potentially confounding factors and derived continuous residual AGRAMMATISM and PARAGRAMMATISM ratings, which we then correlated with the SYNTACTIC COMPREHENSION measure. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$. We supplemented our correlation analyses using Bayesian equivalents, which provide strength of evidence both for and against the null hypothesis.

We performed two types of lesion analyses. First, we ran an analysis across the entire brain using the parcellation developed by Faria et al. (2012), which contains both grey and white matter regions, in NiiStat (www.nitrc.org/projects/niistat/). We used a lesion load threshold of 10% of sample. Therefore, for SYNTACTIC COMPREHENSION, which was assessed in 218 total subjects, we tested regions which were damaged in at least 22 subjects, and for AGRAMMATISM / PARAGRAMMATISM, which was assessed in 53 total subjects, we tested regions which were damaged in at least 5 subjects. Lesion volume was included in all analyses to ensure precise localization (DeMarco & Turkeltaub, 2018; Ivanova et al., 2021). We report analyses permutation-corrected for multiple comparisons across regions (10,000 permutations).

Second, we assessed the extent to which damage to the regions implicated in AGRAMMATISM and PARAGRAMMATISM were associated with SYNTACTIC COMPREHENSION deficits. We first created regions of interest (ROIs) based on the significant results from the atlas-based analyses described above by combining the significant regions together. Thus, for AGRAMMATISM, the ROI consisted of the combination of the inferior frontal gyrus, pars opercularis, the inferior frontal gyrus, pars triangularis, and the posterior middle frontal gyrus, whereas for PARAGRAMMATISM, the ROI consisted of the middle superior temporal gyrus, posterior superior temporal gyrus, and posterior middle temporal gyrus. We then used these lesion distributions as ROIs for further analysis of SYNTACTIC COMPREHENSION. We first calculated proportion damage to each ROI for each of the 218 subjects included in the analysis of SYNTACTIC COMPREHENSION. We adjusted the data using a rationalized arcsine transform (Studebaker, 1985), and then computed residual damage values by covarying out the effect of lesion volume. We then performed non-parametric correlation analyses relating the residual damage values for each ROI and SYNTACTIC COMPREHENSION using Kendall's tau b. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$. We supplemented our correlation analyses using Bayesian equivalents, which provide strength of evidence both for and against the null hypothesis.

Results

Behavioral data

We performed t-tests comparing each group of grammatically-impaired subjects (AGRAMMATIC, PARAGRAMMATIC) to their *not* grammatically-impaired counterparts with respect to our SYNTACTIC COMPREHENSION measure, residual sequential commands scores after variance from auditory word recognition scores was covaried out. Shapiro-Wilk tests for normality indicated a violation of the assumption of normality for the comparison of AGRAMMATIC to not AGRAMMATIC subjects, ($p = 0.868$, $p = 0.032$, respectively), and no violation of the assumption of normality for the comparison of PARAGRAMMATIC to not PARAGRAMMATIC subjects ($p = 0.179$, $p = 0.588$, respectively). Thus, for the comparison of AGRAMMATIC to not AGRAMMATIC subjects we performed a non-parametric Welch's t-test, and for the comparison of PARAGRAMMATIC to not PARAGRAMMATIC subjects we performed a parametric Student's t-test. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$.

The non-parametric Welch's t-test between AGRAMMATIC and not AGRAMMATIC subjects showed a trend towards a significant difference in SYNTACTIC COMPREHENSION, $t(41.569) = 1.499$, $p = 0.071$, whereas the parametric Student's t-test between PARAGRAMMATIC and not PARAGRAMMATIC subjects showed a significant difference in SYNTACTIC COMPREHENSION, $t(51) = 2.525$, $p = 0.007$. Bar charts illustrating the SYNTACTIC COMPREHENSION abilities for each of the groups involved in these comparisons is shown in Figure 2.

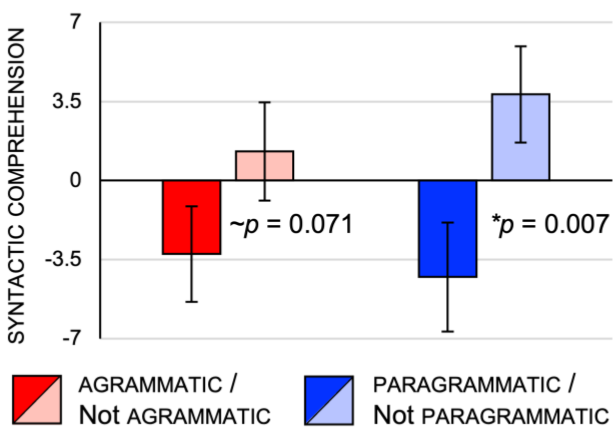

Figure 2. Bar charts of average residual performance on the SYNTACTIC COMPREHENSION measure, for each of the four overlapping groups (AGRAMMATIC, not a AGRAMMATIC, PARAGRAMMATIC, not PARAGRAMMATIC). Error bars indicate standard error of the mean.

Because the group of AGRAMMATIC subjects had much larger lesions than the PARAGRAMMATIC subjects (nearly twice as large, Matchin et al., 2020), we performed one-sided correlation analyses examining the relationship between the residual scores for AGRAMMATISM and PARAGRAMMATISM, incorporating lesion volume as a covariate, with SYNTACTIC COMPREHENSION, using Pearson's rho. We supplemented our frequentist measures with analogous Bayesian analyses. Bayesian measures provide an estimate of the weight of the evidence in favor of one hypothesis or the other, and thus can indicate support for the null hypothesis, unlike standard frequentist measures. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$.

Residual AGRAMMATISM was not associated with lower SYNTACTIC COMPREHENSION, r = -0.00002, p = 0.5. The Bayesian correlation showed moderate evidence in favor of the null hypothesis that no correlation exists, BF_{10} = 0.171, BF_{01} = 5.836. By contrast, we found that residual PARAGRAMMATISM was significantly associated with significantly lower SYNTACTIC COMPREHENSION, r = -0.387, p = 0.002. The Bayesian correlation showed strong evidence for the hypothesis that a correlation exists, BF_{10} = 18.474, and effectively no evidence in favor of the null hypothesis that no correlation exists, BF_{01} = 0.054. Scatterplots illustrating these correlations are shown in Figure 3.

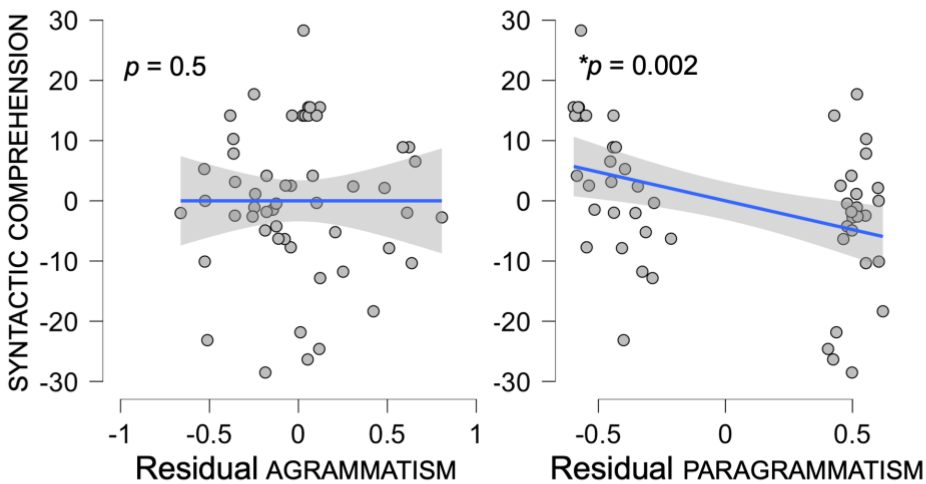

Figure 3. Scatter plots, with fitted linear regression line, of residual SYNTACTIC COMPREHENSION performance, compared to the continuous residual ratings of AGRAMMATISM (left) and PARAGRAMMATISM (right), incorporating lesion volume as a covariate. Shaded area indicates 95% confidence interval.

Lesion data

First, we determined the regions which were significantly associated with each behavioral measure, AGRAMMATISM, PARAGRAMMATISM, and SYNTACTIC COMPREHENSION. For each analysis, we report whole-brain atlas-based analyses in Figure 4. AGRAMMATISM (with lesion volume as a covariate) was associated with damage to the posterior middle frontal gyrus (Z = 4.47), inferior frontal gyrus, pars opercularis (Z = 3.82), and inferior frontal gyrus, pars triangularis (Z = 3.47). PARAGRAMMATISM (with lesion volume as a covariate) was associated with damage to posterior superior temporal gyrus (Z = 3.26), middle superior temporal gyrus (Z = 3.03), and posterior middle temporal gyrus (Z = 2.87). Reduced SYNTACTIC COMPREHENSION was associated with damage to posterior insula (Z = -4.45), middle superior temporal gyrus (Z = -3.58), and posterior superior temporal gyrus (Z = -3.29).

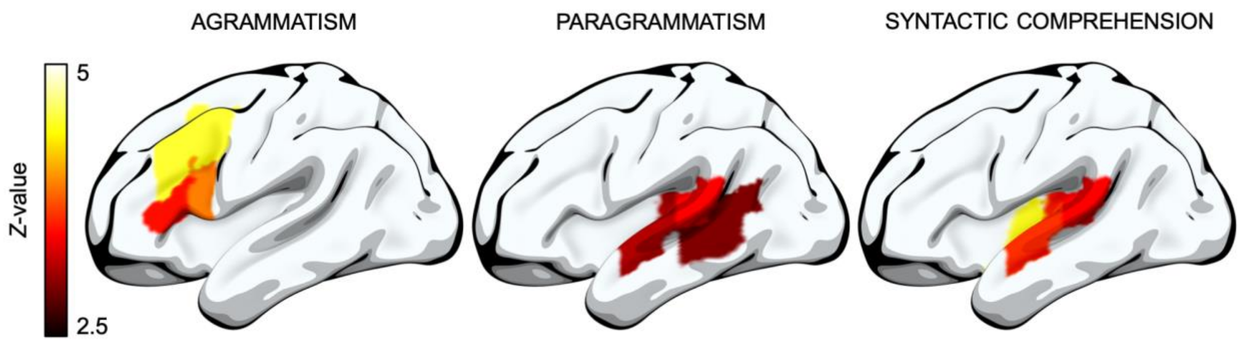

Figure 4. Whole-brain atlas-based analyses, permutation-corrected for multiple comparisons across regions (10,000 permutations). All effects include lesion volume as a covariate. Left: effect of AGRAMMATISM. Middle: effect of PARAGRAMMATISM. Right: effect of SYNTACTIC COMPREHENSION deficits.

We then examined the relationship between SYNTACTIC COMPREHENSION deficits and percent damage to ROIs defined by the regions significantly associated with AGRAMMATISM and PARAGRAMMATISM. Shapiro-Wilk tests for Bivariate Normality indicated a substantial violation of the assumption of normality for the correlation between residual AGRAMMATISM and SYNTACTIC COMPREHENSION ($p = 0.00002$), and for the correlation between residual PARAGRAMMATISM and SYNTACTIC COMPREHENSION ($p = 0.0001$). Therefore, we performed one-sided non-parametric Kendall's Tau B correlation tests. We supplemented our frequentist measures with analogous Bayesian analyses. Bayesian measures provide an estimate of the weight of the evidence in favor of one hypothesis or the other, and thus can indicate support for the null hypothesis, unlike standard frequentist measures. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.025$ for the two comparisons, controlling the total error at $p < 0.05$

We found no significant negative correlation between damage to the AGRAMMATISM ROI and SYNTACTIC COMPREHENSION, Kendall's tau B = -0.024, $p = 0.301$, (Figure 5, left). The Bayesian correlation found moderate evidence in favor of the null hypothesis that the two variables are uncorrelated, $BF_{10} = 0.143$, $BF_{01} = 7$. We found a significant correlation between damage to the PARAGRAMMATISM ROI and SYNTACTIC COMPREHENSION, Kendall's tau B = -0.182, $p = 0.00004$, (Figure 5, right). The Bayesian correlation found very strong evidence in favor of the hypothesis that the two variables are correlated, $BF_{10} = 487.952$, $BF_{01} = 0.002$.

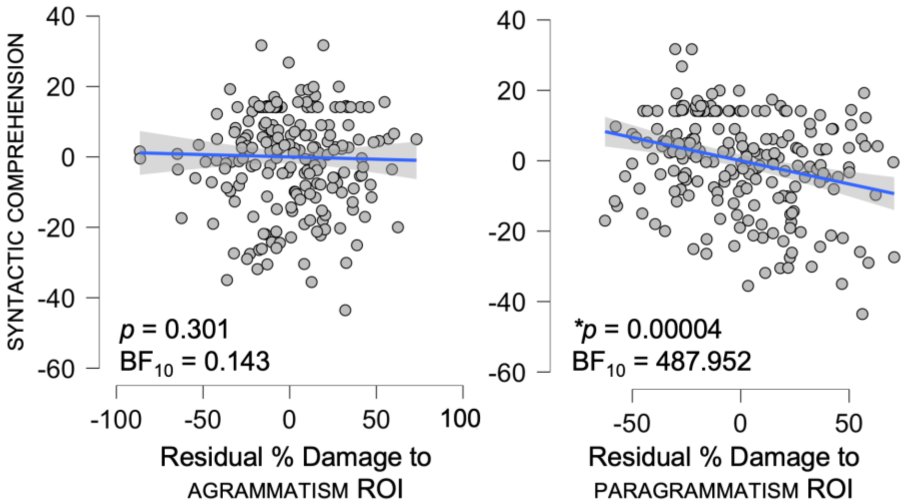

Figure 5. Scatterplots showing the correlations between SYNTACTIC COMPREHENSION deficits and residual percent damage to the ROIs defined by grammatical production deficits, AGRAMMATISM and PARAGRAMMATISM, after incorporating lesion volume as a covariate. LEFT: Plot of the correlation between SYNTACTIC COMPREHENSION deficits and damage to the ROI defined by lesion-symptom analysis of AGRAMMATISM. RIGHT: Plot of the correlation between SYNTACTIC COMPREHENSION and damage to the PARAGRAMMATISM ROI. Shaded areas indicate 95% confidence interval.

Discussion

We found little evidence to support the classical "overarching agrammatism" hypothesis. The presence of expressive AGRAMMATISM was only weakly and not significantly associated with impaired SYNTACTIC COMPREHENSION as assessed by reduced Sequential Commands scores incorporating Auditory Word Recognition scores as a covariate. Given that patients with AGRAMMATISM and frontal damage had lesions much larger than those with damage elsewhere (Matchin et al., 2020), we suspected that previous studies finding associations between agrammatic Broca's aphasia and syntactic comprehension deficits might be due in part to lesions encroaching on the temporal lobe (Fridriksson et al., 2015). When we incorporated lesion volume as a covariate, we found zero correlation between AGRAMMATISM and impaired SYNTACTIC COMPREHENSION. Furthermore, damage to regions associated with AGRAMMATISM (Broca's area and posterior middle frontal gyrus) was not associated with SYNTACTIC COMPREHENSION deficits. Bayesian analyses provided moderate evidence in favor of the null hypothesis, i.e., against the "overarching agrammatism" hypothesis, for both the behavioral and lesion correlations.

By contrast, both our behavioral measure of PARAGRAMMATISM, and damage to the PARAGRAMMATISM ROI (middle and posterior superior temporal gyrus and posterior middle temporal gyrus) were significantly and robustly associated with reduced SYNTACTIC COMPREHENSION. Bayesian analyses provided strong evidence in favor of these associations, i.e. in favor of a grammatical parallelism hypothesis rooted in paragrammatism rather than agrammatism.

While our data speak against the notion of overarching agrammatism, it supports a different form of grammatical parallelism characterized by paragrammatic speech output and significant syntactic comprehension problems. This is caused, we claim, by damage to the same networks for processing hierarchical syntactic structure in the posterior temporal lobe. Thus, it appears as though Wernicke's original hypothesis regarding parallel speech production and comprehension deficits following posterior temporal damage holds for syntax as well. In particular, our results suggest that while both posterior temporal and frontal cortex play important roles in syntax, they do so asymmetrically: posterior temporal cortex is critically involved in both comprehension and production, whereas frontal cortex is only critically involved in production. This supports the framework for syntax in the brain advanced by (Matchin & Hickok, 2020): the posterior temporal lobe (crucially including ventral superior temporal sulcus) underlies a hierarchical lexical syntactic function for interfacing with brain systems involved in processing meaning, whereas the pars triangularis of Broca's area and perhaps a more dorsal region in the middle frontal gyrus underlies a morpho-syntactic sequencing function that interfaces with the motor system.

This finding points to a common neurocomputational architecture for phonological and syntactic systems in the brain, in which frontal regions play a role at these levels predominantly for production while posterior regions play a role in both production and comprehension (Hickok, 2012; Hickok et al., 2011; Matchin & Hickok, 2020). This architecture, in turn, has a deep commonality with the neurocomputational architecture for motor control in which sensory systems define targets for motor planning (Guenther et al., 1998; Hickok, 2014a; Kawato, 1999; Miall & Wolpert, 1996; Perkell, 2012; Shadmehr et al., 2010; Shadmehr & Krakauer, 2008; Wolpert, 1997). The convergence of architectures across linguistic and non-linguistic domains suggests a neurocomputational homology, which may illuminate the evolution and development of language in the brain (Hickok, 2019; Matchin, 2018). However, our results do not imply that we should abandon using the terminology and theoretical postulates of linguistic theory to understand linguistic deficits in aphasia or the neurobiology of language. Rather, what we suggest is that linguistic theory should itself incorporate the distinct computational demands of comprehension and production (Matchin & Hickok, 2020); namely, hierarchical structure and linearization, respectively. This is congruent with some recent linguistic proposals (Berwick & Chomsky, 2016; Idsardi & Raimy, 2013).

Note that the grammatical parallelism hypothesis rooted in paragrammatism and the posterior temporal lobe does not imply that inferior frontal cortex regions never play any role in sentence comprehension. In particular, frontal-motor systems are widely thought to play a key role in working memory (Baddeley, 2003; Baddeley et al., 1981; Pettigrew & Hillis, 2014; Rogalsky et al., 2008). Working memory is important for sentence processing, particularly for difficult constructions and perhaps other demands of everyday communication (false starts and stops, garden-paths/misparsing, preparing to respond to the interlocuter). In particular, the linear morpho-syntactic system in the pars triangularis of Broca's area posited by Matchin & Hickok (2020) is ideal for assisting comprehension by reiterating the heard sequence of morphemes for reanalysis by hierarchical syntactic mechanisms in the posterior temporal lobe. This is congruent with the hypothesis of a syntactic working memory system (Fiebach et al., 2005; Matchin, 2018; Rogalsky et al., 2015) consisting of looping interactions between inferior frontal and posterior temporal cortex. A working memory deficit may help explain some of the observations of associations between agrammatic Broca's aphasia and deficits in the comprehension of semantically reversible, complex, non-canonical sentences.

A role for frontal-motor systems in syntactic working memory may explain some of the syntax-related activations that are observed in inferior frontal cortex in neuroimaging studies (Rogalsky & Hickok, 2011). While early studies found evidence for syntactic comprehension effects primarily in Broca's area, recent neuroimaging studies have found that posterior temporal cortex shows equally (if not more) reliable syntactic comprehension effects (Blank et al., 2016; Brennan et al., 2016; Diachek et al., 2020; Fedorenko et al., 2012, 2016; Goucha & Friederici, 2015; Matchin et al., 2017; Meyer & Friederici, 2016; Nelson et al., 2017; Pallier et al., 2011; Shain et al., 2020; Zaccarella, Meyer, et al., 2017; Zaccarella, Schell, et al., 2017). The fact that both of these regions reliably exhibit syntactic effects is well-explained by attributing a syntactic function to both of these regions (Matchin & Hickok, 2020), with the frontal contribution reflecting production-related morpho-syntactic resources that assist comprehension in demanding contexts, but are not necessary for combining words into structured phrases and sentences, a role reserved for the posterior temporal lobe.

Some lesion-symptom mapping studies have found an association between damage and/or degeneration of inferior frontal cortex and deficits in comprehension of complex, non-canonical sentence structure, typically in addition to posterior temporal damage (Amici et al., 2007; Fridriksson et al., 2018; Kristinsson et al., 2020; Magnusdottir et al., 2013; Mesulam et al., 2015; Tyler et al., 2011; Wilson et al., 2011). However, there are several reasons to question whether these results reflect necessary resources for normal syntactic comprehension. First, all of these studies did not incorporate lesion volume as a covariate, which is an important variable to ensure accurate localization in lesion-symptom mapping (DeMarco & Turkeltaub, 2018; Ivanova et al., 2021), a particularly acute issue given that agrammatic production is associated with large lesions (Matchin et al., 2020) that encroach on the temporal lobe (Fridriksson et al., 2015). Second, many lesion-symptom mapping studies have not reported such an association even for complex structures (Den Ouden et al., 2019; Dronkers et al., 2004; Rogalsky et al., 2018; Thothathiri et al., 2012) (Matchin et al., in review). Third, complex non-canonical structures critically involve substantial working memory resources (King & Just, 1991; Pettigrew & Hillis, 2014; Rogalsky et al., 2008), which could be the source of the associations with frontal networks as noted. Fourth, lesion-symptom mapping of sentence comprehension in general does not highlight Broca's area, but rather posterior temporal and inferior parietal cortex, similar to the areas we identified here (Baldo & Dronkers, 2007; Dronkers et al., 2004; Fridriksson et al., 2018; Pillay et al., 2017; Rogalsky et al., 2018; Thothathiri et al., 2012), and most sentences, regardless of their complexity and canonicity, likely draw on at least some syntactic resources in order to establish the basic thematic relations of sentences. And finally, a lesion symptom mapping study showed that damage to posterior temporal lobe, but not Broca's area, was associated with syntactic acceptability judgment deficits (Wilson & Saygın, 2004). Thus, we believe that the focus on complex, non-canonical structures as measures of syntactic comprehension has been misleading and that future research should focus on syntactic comprehension measures that minimize working memory and other task confounds. We believe our analysis of the sequential commands task, which does not involve complex, noncanonical structures, is a step in the right direction.

Limitations

One of the limitations of this study is that while there was a very strong relationship between damage to the regions implicated in PARAGRAMMATISM and SYNTACTIC COMPREHENSION deficits, the atlas-based analysis of SYNTACTIC COMPREHENSION deficits did not find an association with damage to the posterior middle temporal gyrus. This is the key region posited by (Matchin & Hickok, 2020) to process hierarchical syntactic structure. The key part of the middle temporal gyrus thought to process syntax lies in the ventral bank of the STS, directly adjacent to the superior temporal gyrus, and thus given the somewhat imprecise localization of lesion-symptom mapping the lack of a perfect alignment is not surprising. Additionally, we believe that the SYNTACTIC COMPREHENSION measure, while designed to avert some of the limitations of working memory demands required of complex structures, likely still involved some degree of phonological working memory resources which shifted the lesion distribution superiorly away from the middle temporal gyrus. Future studies should investigate this issue further, developing other measures to determine the more precise relationship to posterior middle temporal gyrus damage and syntactic comprehension deficits.

Conclusions

Overall, we demonstrated the co-incidence of paragrammatic production deficits and syntactic comprehension deficits in aphasia, resulting from common damage to the middle-posterior temporal lobe. Furthermore, we showed no association between agrammatic production and syntactic comprehension deficits, and no association between damage to brain regions implicated in agrammatism (middle and inferior frontal cortex) and syntactic comprehension deficits. Clinically speaking, a new focus should be placed on syntactic abilities in fluent aphasia (both production and comprehension), and that syntactic comprehension in nonfluent aphasia is likely more intact than previously assumed. Theoretically, this provides strong evidence regarding the distinct syntactic functions between Broca’s area and the posterior temporal lobe postulated by Matchin & Hickok (2020).

Acknowledgments

We would like to thank Leigh Ann Spell, Allison Croxton, Anna Doyle, Michele Martin, Katie Murphy, and Sara Sayers for their assistance with data collection, and graduate student clinicians in the Aphasia Lab for transcribing and coding speech samples. This research was supported by the following grants awarded to Julius Fridriksson: National Institute on Deafness and Other Communication Disorders, P50 DC014664, and U01 DC011739, and to Alexandra Basilakos, National Institute on Deafness and Other Communication Disorders T32 DC 014435.

References

Amici, S., Brambati, S. M., Wilkins, D. P., Ogar, J., Dronkers, N. L., Miller, B. L., & Gorno-Tempini, M. L. (2007). Anatomical Correlates of Sentence Comprehension and Verbal Working Memory in Neurodegenerative Disease. *Journal of Neuroscience*, *27*(23), 6282–6290. https://doi.org/10.1523/JNEUROSCI.1331-07.2007

Arbib, M. A. (2016). Towards a Computational Comparative Neuroprimatology: Framing the language-ready brain. *Physics of Life Reviews*, *16*, 1–54. https://doi.org/10.1016/j.plrev.2015.09.003

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*(10), 829–839. https://doi.org/10.1038/nrn1201

Baddeley, A., Eldridge, M., & Lewis, V. (1981). The Role of Subvocalisation in Reading. *The Quarterly Journal of Experimental Psychology Section A*, *33*(4), 439–454. https://doi.org/10.1080/14640748108400802

Baldo, J. V., & Dronkers, N. F. (2007). Neural correlates of arithmetic and language comprehension: A common substrate? *Neuropsychologia*, *45*(2), 229–235. https://doi.org/10.1016/j.neuropsychologia.2006.07.014

Behroozmand, R., Shebek, R., Hansen, D. R., Oya, H., Robin, D. A., Howard, M. A., & Greenlee, J. D. W. (2015). Sensory–motor networks involved in speech production and motor control: An fMRI study. *NeuroImage*, *109*, 418–428. https://doi.org/10.1016/j.neuroimage.2015.01.040

Berndt, R. S., & Caramazza, A. (1980). A redefinition of the syndrome of Broca's aphasia: Implications for a neuropsychological model of language. *Applied Psycholinguistics*, *1*(3), 225–278. https://doi.org/10.1017/S0142716400000552

Berwick, R. C., & Chomsky, N. (2016). *Why only us: Language and evolution*. MIT press.

Blank, I., Balewski, Z., Mahowald, K., & Fedorenko, E. (2016). Syntactic processing is distributed across the language system. *NeuroImage*, *127*, 307–323. https://doi.org/10.1016/j.neuroimage.2015.11.069

Bonhoeffer, C. (1902). Die Riickbildung motorischer Aphasie. *Mitteilung Aus Den Grenzgebieten Der Medizin Und Chirurgie*, *10*, 203.

Bozic, M., Fonteneau, E., Su, L., & Marslen-Wilson, W. D. (2015). Grammatical analysis as a distributed neurobiological function: Bihemispheric Grammatical Analysis. *Human Brain Mapping*, *36*(3), 1190–1201. https://doi.org/10.1002/hbm.22696

Brennan, J. R., Stabler, E. P., Van Wagenen, S. E., Luh, W.-M., & Hale, J. T. (2016). Abstract linguistic structure correlates with temporal activity during naturalistic comprehension. *Brain and Language*, *157–158*, 81–94. https://doi.org/10.1016/j.bandl.2016.04.008

Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D'Esposito, M., & 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. https://doi.org/10.1016/j.bandl.2010.12.001

Butterworth, B., & Howard, D. (1987). Paragrammatisms. *Cognition*, *26*(1), 1–37. https://doi.org/10.1016/0010-0277(87)90012-6

Caramazza, A., & Zurif, E. B. (1976). Dissociation of algorithmic and heuristic processes in language comprehension: Evidence from aphasia. *Brain and Language*, *3*(4), 572–582. https://doi.org/10.1016/0093-934X(76)90048-1

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. MIT Press.

Dapretto, M., & Bookheimer, S. Y. (1999). Form and Content: Dissociating Syntax and Semantics in Sentence Comprehension. *Neuron*, *24*, 427–432.

D'Ausilio, A., Craighero, L., & Fadiga, L. (2012). The contribution of the frontal lobe to the perception of speech. *Journal of Neurolinguistics*, *25*(5), 328–335. https://doi.org/10.1016/j.jneuroling.2010.02.003

DeLeon, J., Gottesman, R. F., Kleinman, J. T., Newhart, M., Davis, C., Heidler-Gary, J., Lee, A., & Hillis, A. E. (2007). Neural regions essential for distinct cognitive processes underlying picture naming. *Brain*, *130*(5), 1408–1422. https://doi.org/10.1093/brain/awm011

Dell, G. S., Schwartz, M. F., Nozari, N., Faseyitan, O., & Branch Coslett, H. (2013). Voxel-based lesion-parameter mapping: Identifying the neural correlates of a computational model of word production. *Cognition*, *128*(3), 380–396. https://doi.org/10.1016/j.cognition.2013.05.007

DeMarco, A. T., & Turkeltaub, P. E. (2018). A multivariate lesion symptom mapping toolbox and examination of lesion-volume biases and correction methods in lesion-symptom mapping. *Human Brain Mapping*, *39*(11), 4169–4182. https://doi.org/10.1002/hbm.24289

Den Ouden, D., Malyutina, S., Basilakos, A., Bonilha, L., Gleichgerrcht, E., Yourganov, G., Hillis, A. E., Hickok, G., Rorden, C., & Fridriksson, J. (2019). Cortical and structural-connectivity damage correlated with impaired syntactic processing in aphasia. *Human Brain Mapping*, *40*(7), 2153–2173. https://doi.org/10.1002/hbm.24514

Diachek, E., Blank, I., Siegelman, M., Affourtit, J., & Fedorenko, E. (2020). The domain-general multiple demand (MD) network does not support core aspects of language comprehension: A large-scale fMRI investigation. *The Journal of Neuroscience*, JN-RM-2036-19. https://doi.org/10.1523/JNEUROSCI.2036-19.2020

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, *92*(1–2), 145–177. https://doi.org/10.1016/j.cognition.2003.11.002

Embick, D., Marantz, A., Miyashita, Y., O'Neil, W., & Sakai, K. L. (2000). A syntactic specialization for Broca's area. *Proceedings of the National Academy of Sciences*, *97*(11), 6150–6154. https://doi.org/10.1073/pnas.100098897

Faria, A. V., Joel, S. E., Zhang, Y., Oishi, K., van Zjil, P. C. M., Miller, M. I., Pekar, J. J., & Mori, S. (2012). Atlas-based analysis of resting-state functional connectivity: Evaluation for reproducibility and multi-modal anatomy–function correlation studies. *NeuroImage*, *61*(3), 613–621. https://doi.org/10.1016/j.neuroimage.2012.03.078

Fedorenko, E., Nieto-Castañon, A., & Kanwisher, N. (2012). Lexical and syntactic representations in the brain: An fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia*, *50*(4), 499–513. https://doi.org/10.1016/j.neuropsychologia.2011.09.014

Fedorenko, E., Scott, T. L., Brunner, P., Coon, W. G., Pritchett, B., Schalk, G., & Kanwisher, N. (2016). Neural correlate of the construction of sentence meaning. *Proceedings of the National Academy of Sciences*, *113*(41), E6256–E6262. https://doi.org/10.1073/pnas.1612132113

Fiebach, C. J., Schlesewsky, M., Lohmann, G., von Cramon, D. Y., & Friederici, A. D. (2005). Revisiting the role of Broca's area in sentence processing: Syntactic integration versus syntactic working memory. *Human Brain Mapping*, *24*(2), 79–91. https://doi.org/10.1002/hbm.20070

Fridriksson, J., Bonilha, L., & Rorden, C. (2007). Severe Broca's Aphasia without Broca's Area Damage. *Behavioural Neurology*, *18*(4), 237–238. https://doi.org/10.1155/2007/785280

Fridriksson, J., den Ouden, D.-B., Hillis, A. E., Hickok, G., Rorden, C., Basilakos, A., Yourganov, G., & Bonilha, L. (2018). Anatomy of aphasia revisited. *Brain*, *141*(3), 848–862. https://doi.org/10.1093/brain/awx363

Fridriksson, J., Fillmore, P., Guo, D., & Rorden, C. (2015). Chronic Broca's Aphasia Is Caused by Damage to Broca's and Wernicke's Areas. *Cerebral Cortex*, *25*(12), 4689–4696. https://doi.org/10.1093/cercor/bhu152

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*(2), 78–84. https://doi.org/10.1016/S1364-6613(00)01839-8

Friederici, A. D. (2017). *Language in our brain: The origins of a uniquely human capacity*. MIT Press.

Friederici, A. D., Meyer, M., & von Cramon, D. Y. (2000). Auditory Language Comprehension: An Event-Related fMRI Study on the Processing of Syntactic and Lexical Information. *Brain and Language*, *74*(2), 289–300. https://doi.org/10.1006/brln.2000.2313

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. https://doi.org/10.1126/science.170.3961.940

Geschwind, N. (1972). Language and the Brain. *Scientific American*, *226*(4), 76–83.

Geschwind, N. (1979). Specializations of the Human Brain. *Scientific American*, *241*(3), 180–199. https://doi.org/10.1038/scientificamerican0979-180

Golfinopoulos, E., Tourville, J. A., Bohland, J. W., Ghosh, S. S., Nieto-Castanon, A., & Guenther, F. H. (2011). FMRI investigation of unexpected somatosensory feedback perturbation during speech. *NeuroImage*, *55*(3), 1324–1338. https://doi.org/10.1016/j.neuroimage.2010.12.065

Goodglass, H., Christensen, J. A., & Gallagher, R. (1993). Comparison of morphology and syntax in free narrative and structured tests: Fluent vs. Nonfluent aphasics. *Cortex*, *29*(3), 377–408.

Gorno-Tempini, M. L., Dronkers, N. F., Rankin, K. P., Ogar, J. M., Phengrasamy, L., Rosen, H. J., Johnson, J. K., Weiner, M. W., & Miller, B. L. (2004). Cognition and anatomy in three variants of primary progressive aphasia. *Annals of Neurology*, *55*(3), 335–346. https://doi.org/10.1002/ana.10825

Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca's Area. *NeuroImage*, *114*, 294–302. https://doi.org/10.1016/j.neuroimage.2015.04.011

Guenther, F. H. (2006). Cortical interactions underlying the production of speech sounds. *Journal of Communication Disorders*, *39*(5), 350–365. https://doi.org/10.1016/j.jcomdis.2006.06.013

Guenther, F. H., Hampson, M., & Johnson, D. (1998). A Theoretical Investigation of Reference Frames for the Planning of Speech Movements. *Psychological Review*, *105*, 611–633.

Guenther, F. H., & Hickok, G. (2015). Role of the auditory system in speech production. In *Handbook of Clinical Neurology* (Vol. 129, pp. 161–175). Elsevier. https://doi.org/10.1016/B978-0-444-62630-1.00009-3

Guenther, F. H., & Hickok, G. (2016). Neural Models of Motor Speech Control. In *Neurobiology of Language* (pp. 725–740). Elsevier. https://doi.org/10.1016/B978-0-12-407794-2.00058-4

Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, *9*(9), 416–423. https://doi.org/10.1016/j.tics.2005.07.004

Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00416

Hagoort, P. (2016). MUC (Memory, Unification, Control). In *Neurobiology of Language* (pp. 339–347). Elsevier. https://doi.org/10.1016/B978-0-12-407794-2.00028-6

Hagoort, P., & Indefrey, P. (2014). The Neurobiology of Language Beyond Single Words. *Annual Review of Neuroscience*, *37*(1), 347–362. https://doi.org/10.1146/annurev-neuro-071013-013847

Heeschen, C. (1985). Agrammatism versus paragrammatism: A fictitious opposition. In M.-L. Kean (Ed.), *Agrammatism* (pp. 207–248). Academic Press.

Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, *13*(2), 135–145. https://doi.org/10.1038/nrn3158

Hickok, G. (2014a). *The myth of mirror neurons: The real neuroscience of communication and cognition*. WW Norton & Company.

Hickok, G. (2014b). The architecture of speech production and the role of the phoneme in speech processing. *Language, Cognition and Neuroscience*, *29*(1), 2–20. https://doi.org/10.1080/01690965.2013.834370

Hickok, G. (2019). *Neuro-Architectural Homologies for Language in the Human and Non-Human Primate Brain*. Center for the Study of Aphasia Recovery, University of South Carolina. https://www.youtube.com/watch?v=LRE_nSie1mE

Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory–Motor Interaction Revealed by fMRI: Speech, Music, and Working Memory in Area Spt. *Journal of Cognitive Neuroscience*, *15*(5), 10.

Hickok, G., Houde, J., & Rong, F. (2011). Sensorimotor Integration in Speech Processing: Computational Basis and Neural Organization. *Neuron*, *69*(3), 407–422. https://doi.org/10.1016/j.neuron.2011.01.019

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences*, *4*(4), 131–138. https://doi.org/10.1016/S1364-6613(00)01463-7

Hillis, A. E., Kleinman, J. T., Newhart, M., J. Heidler-Gary, Gottesman, R., Barker, P. B., Aldrich, E., Llinas, R., Wityk, R., & Chaudhry, P. (2006). Restoring Cerebral Blood Flow Reveals Neural Regions Critical for Naming. *Journal of Neuroscience*, *26*(31), 8069–8073. https://doi.org/10.1523/JNEUROSCI.2088-06.2006

Hillis, A. E., Wityk, R. J., Tuffiash, E., Beauchamp, N. J., Jacobs, M. A., Barker, P. B., & Selnes, O. A. (2001). Hypoperfusion of Wernicke's area predicts severity of semantic deficit in acute stroke. *Annals of Neurology*, *50*(5), 561–566. https://doi.org/10.1002/ana.1265

Idsardi, W., & Raimy, E. (2013). Three types of linearization and the temporal aspects of speech. In T. Biberauer & I. Roberts (Eds.), *Challenges to Linearization*. DE GRUYTER. https://doi.org/10.1515/9781614512431.31

Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition*, *92*(1–2), 101–144. https://doi.org/10.1016/j.cognition.2002.06.001

Ivanova, M. V., Herron, T. J., Dronkers, N. F., & Baldo, J. V. (2021). An empirical comparison of univariate versus multivariate methods for the analysis of brain–behavior mapping. *Human Brain Mapping*, *42*, 1070–1101.

Jakobson, R. (1956). Two aspects of language and two types of aphasic disturbances. In R. Jakobson & M. Halle (Eds.), *Fundamentals of Language* (pp. 115–133). Mouton.

Jakobson, R., & Halle, M. (1956). *Fundamentals of language*. Mouton.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*(6), 718–727. https://doi.org/10.1016/S0959-4388(99)00028-8

Kean, M.-L. (1977). The linguistic interpretation of aphasic syndromes: Agrammatism in Broca's aphasia, an example. *Cognition*, *5*(1), 9–46. https://doi.org/10.1016/0010-0277(77)90015-4

Kean, M.-L. (1995). The Elusive Character of Agrammatism. *Brain and Language*, *50*, 369–384.

Kertesz, A. (2007). *Western Aphasia Battery- Revised*. Grune and Stratton.

King, J., & Just, M. A. (1991). Individual differences in syntactic processing: The role of working memory. *Journal of Memory and Language*, *30*(5), 580–602. https://doi.org/10.1016/0749-596X(91)90027-H

Kleist, K. (1914). Aphasie und geisteskrankheit. *Münchener Medizinische Wochenschrift*, *6*, 8–12.

Kristinsson, S., Thors, H., Yourganov, G., Magnusdottir, S., Hjaltason, H., Stark, B. C., Basilakos, A., den Ouden, D.-B., Bonilha, L., Rorden, C., Hickok, G., Hillis, A., & Fridriksson, J. (2020). Brain Damage Associated with Impaired Sentence Processing in Acute Aphasia. *Journal of Cognitive Neuroscience*, *32*(2), 256–271. https://doi.org/10.1162/jocn_a_01478

Kuperberg, G. R. (2007). Neural mechanisms of language comprehension: Challenges to syntax. *Brain Research*, *1146*, 23–49. https://doi.org/10.1016/j.brainres.2006.12.063

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (De)constructing the N400. *Nature Reviews Neuroscience*, *9*(12), 920–933. https://doi.org/10.1038/nrn2532

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

Levelt, W. J. M. (2001). Spoken word production: A theory of lexical access. *Proceedings of the National Academy of Sciences*, *98*(23), 13464–13471. https://doi.org/10.1073/pnas.231459498

Levelt, W. J. M., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *BEHAVIORAL AND BRAIN SCIENCES*, 76.

Linebarger, M. C., Schwartz, M. F., & Saffran, E. M. (1983). Sensitivity to grammatical structure in so-called agrammatic aphasics. *Cognition*, *13*(3), 361–392. https://doi.org/10.1016/0010-0277(83)90015-X

MacWhinney, B., Fromm, D., Forbes, M., & Holland, A. (2011). AphasiaBank: Methods for studying discourse. *Aphasiology*, *25*(11), 1286–1307. https://doi.org/10.1080/02687038.2011.589893

Magnusdottir, S., Fillmore, P., den Ouden, D. B., Hjaltason, H., Rorden, C., Kjartansson, O., Bonilha, L., & Fridriksson, J. (2013). Damage to left anterior temporal cortex predicts impairment of complex syntactic processing: A lesion-symptom mapping study: ATL Damage Impairs Complex Syntax Processing. *Human Brain Mapping*, *34*(10), 2715–2723. https://doi.org/10.1002/hbm.22096

Matchin, W. (2018). A neuronal retuning hypothesis of sentence-specificity in Broca's area. *Psychonomic Bulletin & Review*, *25*(5), 1682–1694. https://doi.org/10.3758/s13423-017-1377-6

Matchin, W., Basilakos, A., Stark, B. C., den Ouden, D.-B., Fridriksson, J., & Hickok, G. (2020). Agrammatism and paragrammatism: A cortical double dissociation revealed by lesion-symptom mapping. *Neurobiology of Language*, 1–47. https://doi.org/10.1162/nol_a_00010

Matchin, W., Brodbeck, C., Hammerly, C., & Lau, E. (2019). The temporal dynamics of structure and content in sentence comprehension: Evidence from fMRI-constrained MEG. *Human Brain Mapping*, *40*(2), 663–678. https://doi.org/10.1002/hbm.24403

Matchin, W., Hammerly, C., & Lau, E. (2017). The role of the IFG and pSTS in syntactic prediction: Evidence from a parametric study of hierarchical structure in fMRI. *Cortex*, *88*, 106–123. https://doi.org/10.1016/j.cortex.2016.12.010

Matchin, W., & Hickok, G. (2020). The Cortical Organization of Syntax. *Cerebral Cortex*, *30*(3), 1481–1498.

Matchin, W., Liao, C.-H., Gaston, P., & Lau, E. (2019). Same words, different structures: An fMRI investigation of argument relations and the angular gyrus. *Neuropsychologia*, *125*, 116–128. https://doi.org/10.1016/j.neuropsychologia.2019.01.019

Matchin, W., & Rogalsky, C. (in press). Aphasia and Syntax. In J. Sprouse (Ed.), *Handbook of Experimental Syntax*. Oxford University Press. https://psyarxiv.com/m8pnd/

Matchin, W., & 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*, 1–12. https://doi.org/10.1093/texcom/tgaa029

Menenti, L., Gierhan, S. M. E., Segaert, K., & 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. https://doi.org/10.1177/0956797611418347

Mesulam, M.-M., Thompson, C. K., Weintraub, S., & Rogalski, E. J. (2015). The Wernicke conundrum and the anatomy of language comprehension in primary progressive aphasia. *Brain*, *138*(8), 2423–2437. https://doi.org/10.1093/brain/awv154

Meyer, L., & Friederici, A. D. (2016). Neural Systems Underlying the Processing of Complex Sentences. In G. Hickok & S. L. Small (Eds.), *Neurobiology of Language* (pp. 597–606). Elsevier. https://doi.org/10.1016/B978-0-12-407794-2.00048-1

Miall, R. C., & Wolpert, D. M. (1996). Forward Models for Physiological Motor Control. *Neural Networks*, *9*(8), 1265–1279. https://doi.org/10.1016/S0893-6080(96)00035-4

Mohr, J. P., Pessin, M. S., Finkelstein, S., Funkenstein, H. H., Duncan, G. W., & Davis, K. R. (1978). Broca aphasia: Pathologic and clinical. *Neurology*, *28*(4), 311–311. https://doi.org/10.1212/WNL.28.4.311

Momma, S., & Phillips, C. (2018). The Relationship Between Parsing and Generation. *Annual Review of Linguistics*, *4*(1), 233–254. https://doi.org/10.1146/annurev-linguistics-011817-045719

Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F., & Fazio, F. (2001). Syntax and the Brain: Disentangling Grammar by Selective Anomalies. *NeuroImage*, *13*(1), 110–118. https://doi.org/10.1006/nimg.2000.0668

Nelson, M. J., El Karoui, I., Giber, K., Yang, X., Cohen, L., Koopman, H., Cash, S. S., Naccache, L., Hale, J. T., Pallier, C., & Dehaene, S. (2017). Neurophysiological dynamics of phrase-structure building during sentence processing. *Proceedings of the National Academy of Sciences*, *114*(18), E3669–E3678. https://doi.org/10.1073/pnas.1701590114

Ocampo, B., & Kritikos, A. (2011). Interpreting actions: The goal behind mirror neuron function. *Brain Research Reviews*, *67*(1–2), 260–267. https://doi.org/10.1016/j.brainresrev.2011.03.001

Ogar, J. M., Baldo, J. V., Wilson, S. M., Brambati, S. M., Miller, B. L., Dronkers, N. F., & Gorno-Tempini, M. L. (2011). Semantic dementia and persisting Wernicke's aphasia: Linguistic and anatomical profiles. *Brain and Language*, *117*(1), 28–33. https://doi.org/10.1016/j.bandl.2010.11.004

Pallier, C., Devauchelle, A.-D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences*, *108*(6), 2522–2527. https://doi.org/10.1073/pnas.1018711108

Perkell, J. S. (2012). Movement goals and feedback and feedforward control mechanisms in speech production. *Journal of Neurolinguistics*, *25*(5), 382–407. https://doi.org/10.1016/j.jneuroling.2010.02.011

Pettigrew, C., & Hillis, A. E. (2014). Role for memory capacity in sentence comprehension: Evidence from acute stroke. *Aphasiology*, *28*(10), 1258–1280. https://doi.org/10.1080/02687038.2014.919436

Pillay, S. B., Binder, J. R., Humphries, C., Gross, W. L., & Book, D. S. (2017). Lesion localization of speech comprehension deficits in chronic aphasia. *Neurology*, *88*(10), 970–975. https://doi.org/10.1212/WNL.0000000000003683

Pinker, S., & Ullman, M. T. (2002). The past and future of the past tense. *Trends in Cognitive Sciences*, *6*(11), 456–463. https://doi.org/10.1016/S1364-6613(02)01990-3

Pulvermüller, F., & Fadiga, L. (2010). Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, *11*(5), 351–360. https://doi.org/10.1038/nrn2811

Rilling, J. K. (2014). Comparative primate neurobiology and the evolution of brain language systems. *Current Opinion in Neurobiology*, *28*, 10–14. https://doi.org/10.1016/j.conb.2014.04.002

Rogalsky, C., Almeida, D., Sprouse, J., & 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. https://doi.org/10.1080/23273798.2015.1066831

Rogalsky, C., & Hickok, G. (2011). The Role of Broca's Area in Sentence Comprehension. *Journal of Cognitive Neuroscience*, *23*(7), 17.

Rogalsky, C., LaCroix, A. N., Chen, K.-H., Anderson, S. W., Damasio, H., Love, T., & Hickok, G. (2018). The Neurobiology of Agrammatic Sentence Comprehension: A Lesion Study. *Journal of Cognitive Neuroscience*, *30*(2), 234–255. https://doi.org/10.1162/jocn_a_01200

Rogalsky, C., Matchin, W., & Hickok, G. (2008). Broca's area, sentence comprehension, and working memory: An fMRI study. *Frontiers in Human Neuroscience*, *2*, 1–13. https://doi.org/10.3389/neuro.09.014.2008

Saffran, E. M., Schwartz, M. F., & Marin, O. S. M. (1980). The word order problem in agrammatism: II. Production. *Brain and Language*, *10*(2), 263–280. https://doi.org/10.1016/0093-934X(80)90056-5

Sapolsky, D., Bakkour, A., Negreira, A., Nalipinski, P., Weintraub, S., Mesulam, M.-M., Caplan, D., & Dickerson, B. C. (2010). Cortical neuroanatomic correlates of symptom severity in primary progressive aphasia. *Neurology*, *75*(4), 358–366. https://doi.org/10.1212/WNL.0b013e3181ea15e8

Schwartz, M. F., Saffran, E. M., & Marin, O. S. M. (1980). The Word Order Problem in Agrammatism. I. Comprehension. *Brain and Language*, *10*, 249–262.

Shadmehr, R., & Krakauer, J. W. (2008). A computational neuroanatomy for motor control. *Experimental Brain Research*, *185*(3), 359–381. https://doi.org/10.1007/s00221-008-1280-5

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error Correction, Sensory Prediction, and Adaptation in Motor Control. *Annual Review of Neuroscience*, *33*(1), 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135

Shain, C., Blank, I. A., van Schijndel, M., Schuler, W., & Fedorenko, E. (2020). FMRI reveals language-specific predictive coding during naturalistic sentence comprehension. *Neuropsychologia*, *138*, 107307. https://doi.org/10.1016/j.neuropsychologia.2019.107307

Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of Syntactic Comprehension by Positron Emission Tomography. *Brain and Language*, *52*(24), 452–473.

Studebaker, G. A. (1985). A “Rationalized” Arcsine Transform. *Journal of Speech and Hearing Research*, *28*(03), 455–462.

Swinney, D., & Zurif, E. (1995). Syntactic processing in aphasia. *Brain and Language*, *50*, 225–239.

Thothathiri, M., Kimberg, D. Y., & Schwartz, M. F. (2012). The Neural Basis of Reversible Sentence Comprehension: Evidence from Voxel-based Lesion Symptom Mapping in Aphasia. *Journal of Cognitive Neuroscience*, *24*(1), 212–222. https://doi.org/10.1162/jocn_a_00118

Tourville, J. A., Reilly, K. J., & Guenther, F. H. (2008). Neural mechanisms underlying auditory feedback control of speech. *NeuroImage*, *39*(3), 1429–1443. https://doi.org/10.1016/j.neuroimage.2007.09.054

Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., Papoutsi, M., & Stamatakis, E. A. (2011). Left inferior frontal cortex and syntax: Function, structure and behaviour in patients with left hemisphere damage. *Brain*, *134*(2), 415–431. https://doi.org/10.1093/brain/awq369

Tyler, L. K., Shafto, M. A., Randall, B., Wright, P., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010). Preserving Syntactic Processing across the Adult Life Span: The Modulation of the Frontotemporal Language System in the Context of Age-Related Atrophy. *Cerebral Cortex*, *20*(2), 352–364. https://doi.org/10.1093/cercor/bhp105

von Humboldt, W. (1836). *On language*. Cambridge University Press.

Wernicke, C. (1874). The symptom complex of aphasia: A psychological study on an anatomical basis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Boston studies in the philosophy of science* (pp. 34–97). D. Reidel Publishing Company.

Wilson, S. M., Dronkers, N. F., Ogar, J. M., Jang, J., Growdon, M. E., Agosta, F., Henry, M. L., Miller, B. L., & Gorno-Tempini, M. L. (2010). Neural Correlates of Syntactic Processing in the Nonfluent Variant of Primary Progressive Aphasia. *Journal of Neuroscience*, *30*(50), 16845–16854. https://doi.org/10.1523/JNEUROSCI.2547-10.2010

Wilson, S. M., Galantucci, S., Tartaglia, M. C., Rising, K., Patterson, D. K., Henry, M. L., Ogar, J. M., DeLeon, J., Miller, B. L., & Gorno-Tempini, M. L. (2011). Syntactic Processing Depends on Dorsal Language Tracts. *Neuron*, *72*(2), 397–403. https://doi.org/10.1016/j.neuron.2011.09.014

Wilson, S. M., Henry, M. L., Besbris, M., Ogar, J. M., Dronkers, N. F., Jarrold, W., Miller, B. L., & Gorno-Tempini, M. L. (2010). Connected speech production in three variants of primary progressive aphasia. *Brain*, *133*(7), 2069–2088. https://doi.org/10.1093/brain/awq129

Wilson, S. M., & Saygın, A. P. (2004). Grammaticality Judgment in Aphasia: Deficits Are Not Specific to Syntactic Structures, Aphasic Syndromes, or Lesion Sites. *Journal of Cognitive Neuroscience*, *16*(2), 238–252. https://doi.org/10.1162/089892904322984535

Wolpert, M. (1997). Computational approaches control. *Trends in Cognitive Sciences*, *1*(6), 209–216.

Wulfeck, B., & Bates, E. (1991). Differential Sensitivity to Errors of Agreement and Word Order in Broca's Aphasia. *Journal of Cognitive Neuroscience*, *3*(3), 258–272. https://doi.org/10.1162/jocn.1991.3.3.258

Yagata, S. A., Yen, M., McCarron, A., Bautista, A., Lamair-Orosco, G., & Wilson, S. M. (2017). Rapid recovery from aphasia after infarction of Wernicke's area. *Aphasiology*, *31*(8), 951–980. https://doi.org/10.1080/02687038.2016.1225276

Zaccarella, E., Meyer, L., Makuuchi, M., & Friederici, A. D. (2017). Building by Syntax: The Neural Basis of Minimal Linguistic Structures. *Cerebral Cortex*, *27*(1), 1–11. https://doi.org/10.1093/cercor/bhv234

Zaccarella, E., Schell, M., & Friederici, A. D. (2017). Reviewing the functional basis of the syntactic Merge mechanism for language: A coordinate-based activation likelihood estimation meta-analysis. *Neuroscience & Biobehavioral Reviews*, *80*, 646–656. https://doi.org/10.1016/j.neubiorev.2017.06.011

Zurif, E. B. (1980). Language Mechanisms: A Neuropsychological Perspective: The effects of focal brain damage on the processing of syntactic elements may provide an important clue to the manner in which language is organized in the brain. *American Scientist*, *68*(3), 305–311.

Zurif, E. B., Caramazza, A., & Myerson, R. (1972). Grammatical Judgments of Agrammatic Aphasics. *Neuropsychologia*, *10*, 405–417.