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Abstract linguistic structure correlates with temporal activity during naturalistic comprehension

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ABSTRACT

Neurolinguistic accounts of sentence comprehension identify a network of relevant brain regions, but do not detail the information flowing through them. We investigate syntactic information. Does brain activity implicate a computation over hierarchical grammars or does it simply reflect linear order, as in a Markov chain? To address this question, we quantify the cognitive states implied by alternative parsing models. We compare processing-complexity predictions from these states against fMRI timecourses from regions that have been implicated in sentence comprehension. We find that hierarchical grammars independently predict timecourses from left anterior and posterior temporal lobe. Markov models are predictive in these regions and across a broader network that includes the inferior frontal gyrus. These results suggest that while linear effects are wide-spread across the language network, certain areas in the left temporal lobe deal with abstract, hierarchical syntactic representations.

1. Introduction

The neural bases of syntactic processing remain elusive, despite intensive study. Current models catalog the network of regions and connections involved in various sentence-related computations, including syntax, but do not specify the kind of information that flows through this network (see e.g. Friederici & Gierhan, 2013; Hagoort & Indefrey, 2014; Hickok & Poeppel, 2007; Turken & Dronkers, 2011). As Poeppel (2012) notes, it is the information encoded during incremental stages of language comprehension that is critical for mapping between the vocabulary of neurobiology and the vocabulary of linguistics. This study examines what kind of syntactic information is manipulated by brain regions involved in sentence comprehension by correlating the complexity of different syntactic structures with brain activity recorded using fMRI while participants listen to a naturalistic narrative.

The proper conception of syntactic structure is debated across the language sciences. The available models range across many different levels of detail. There are models based on word-to-word dependencies, models based on abstract, hierarchical grammars, and many alternatives in between. While mathematical linguists are in agreement regarding the level of expressive power needed for adequate natural language grammars (Joshi, Shanker, & Weir, 1990; Shieber, 1985; Stabler, 2013a) there remains a debate over the need for more abstract representations in every-day language performance (Frank & Bod, 2011; Sanford & Sturt, 2002). To address this debate, we quantify, word-by-word, the cognitive states that are implied by parsing models that assign comparatively more or less detailed syntactic analyses. We evaluate alternative theories of syntactic structure and parsing by fitting these models to brain activity from regions that have been traditionally associated with sentence comprehension. By relying on brain data collected while participants simply listen to a story, we aim to better understand the role of syntax in every-day language comprehension.

1.1. Brain regions involved in syntactic processing

The spatio-temporal characteristics of brain activity that is sensitive to sentence structure have been examined using a wide variety of experimental techniques (see Hagoort & Indefrey, 2014 for a recent review). One common approach has been to vary whether

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syntactic structure is present or not by comparing phrases or sentences with lists of words. Sentence structure reliably leads to greater activation in the anterior portion of the temporal lobes (ATL) across multiple techniques and stimulus modalities (Brennan & Pylkkänen, 2012; Friederici, Opitz, & von Cramon, 2000; Humphries, Binder, Medler, & Liebenthal, 2006; Jobard, Vigneau, Mazoyer, & Tzourio-Mazoyer, 2007; Rogalsky & Hickok, 2009; Snijders et al., 2009; Stowe et al., 1998; Vandenberghe, Nobre, & Price, 2002; Xu, Kemeny, Park, Frattali, & Braun, 2005). Many studies also show sensitivity in a broader network as well, which includes the left inferior frontal gyrus (IFG; "Broca's Area") and the posterior temporal lobe (PTL; "Wernicke's Area") in the vicinity of the temporal-parietal junction (Brennan & Pylkkänen, 2012; Friederici et al., 2000; Jobard et al., 2007; Pallier, Devauchelle, & Dehaene, 2011; Snijders et al., 2009; Vandenberghe et al., 2002; Xu et al., 2005).

These studies reveal a network of regions that are sensitive to sentence structure, with a focus on the ATL, the IFG and the PTL. Evidence suggests that these regions subserve different functions that relate to identifying or perhaps interpreting phrases, though debate is far from settled. In several of these studies, the ATL, but not the IFG or PTL, is activated even for simple sentences (Rogalsky & Hickok, 2009; Stowe et al., 1998), though others show broader activations (e.g. Pallier et al., 2011; Snijders et al., 2009). Further work using Magnetoencephalography (MEG) has shown that simple two-word phrases lead to increased ATL activation within 200–400 ms of word onset in both visual and auditory presentation (Bemis & Pylkkänen, 2011; Bemis & Pylkkänen, 2013). This effect generalizes across languages and phrase types (Westerlund, Kastner, Al Kaabi, & Pylkkänen, 2015). Shetreet, Friedmann, and Hadar (2009) report a similar sensitivity to constituent structure type in the anterior temporal lobe: more complex hierarchical structure (phrasal vs. nominal verb complements) increased activation in this region. Brennan et al. (2012) build on these observations by testing for sensitivity to incremental, word-by-word, phrase-structure complexity. In this study, the ATL is the only brain area whose activity correlates positively with phrase-structure complexity. Some models suggest that the ATL may subserve constituent structure processes, a conclusion consistent with the morphosyntactic deficits due to anterior lesions observed by Dronkers, Wilkins, Van Valin, Redfern, and Jaeger (2004) (e.g. Friederici & Gierhan, 2013). However, more recent evidence from magnetoencephalography (Westerlund & Pylkkänen, 2014; Zhang & Pylkkänen, 2015) and patient studies of Primary Progressive Aphasia (Wilson et al., 2014) point towards a more nuanced function that relates to the semantic interpretation of composed structures.

Turning to the functional role of the PTL, it has been reported to be modulated by the presence or absence of basic phrase structure in some studies (e.g. Bemis & Pylkkänen, 2013; Pallier et al., 2011), but does not uniformly show such effects across the literature. There is also evidence from neurodegenerative disorders that posterior temporal and inferior parietal atrophy is associated with syntactic deficits (Wilson et al., 2011). Some theorists have hypothesized that this region may play a role in discourse-level comprehension (e.g. Ferstl, Neumann, Bogler, & Yves von Cramon, 2008), though note also that nodes within this broad area, specifically along the posterior middle temporal gyrus, have long been implicated in lexical processing that is sensitive to sentence and discourse context (see Hickok & Poeppel, 2007, for discussion). Bornkessel-Schlesewsky, Schlesewsky, Small, and Rauschecker (2015) argue that posterior and dorsal regions, which include the PTL and extend through the inferior parietal lobule (IPL) to premotor cortex, are involved in sentence processing that is sensitive to linear order. These order-sensitive regions contrast with ventral anterior regions like the ATL, discussed above, which are associated with hierarchical processes. It remains unknown whether sentence-related activation in PTL is best attributed to a single function, such as order-related, lexical, or discourse computations, or to some combination of these or other functions.

Evidence for a functional division specifically between temporal lobe processing and the IFG comes from studies that compare processing of sentence types which differ in their constituent structure or dependency properties. Studies that compare sentences which differ in memory-load demands, such as subject and object relative clauses, yield differential activation in IFG, with variation in the precise localization (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Ben-Shachar, Palti, & Grodzinsky, 2004; Caplan, Chen, & Waters, 2008; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Santi & Grodzinsky, 2007a; Santi & Grodzinsky, 2007b; Santi & Grodzinsky, 2010; Stromswold, Caplan, Alpert, & Rauch, 1996;). This result is consistent with deficit-lesion studies suggesting that frontal lobe damage most strongly impacts the processing of syntactically complex sentences (Caramazza & Zurif, 1976; Grodzinsky, 2000; Zurif, 1995). One possibility is that the IFG is implicated in the processing of more complex syntactic operations, such as the formation of long-distance dependencies, however, the literature has yet to settle on a functional explanation that captures the broader range of observations (see Rogalsky & Hickok, 2010, for a critical review). While some models take the IFG to be implicated only in more complex syntactic operations (e.g. Grodzinsky & Friederici, 2006), in others it is positioned as a central hub for basic combinatoric processing (Hagoort, 2013). This latter view contrasts with that described above in which basic combinatorics is attributed to the ATL (e.g. Friederici & Gierhan, 2013). One avenue of current research is whether these disparate results may be reconciled in terms of fine-grained functional divisions within sub-parts of the IFG. For example, Zaccarella and Friederici (2015) report sensitivity in a sub-part of the Pars Opercularis of the IFG to very simple phrases. Similarly, different argument structure configurations have been associated with differences in IFG activation that form a spatial cline (Bornkessel-Schlesewsky & Schlesewsky, 2009).

Despite the lack of consensus about the functional division of anterior-frontal and posterior-dorsal structures in sentence comprehension, a common thread across this broad literature is that the mental representations whose processing is implicated in various regions are described at a relatively coarse-grain, for example, at the level of separating syntactic and compositional semantic representations (Westerlund & Pylkkänen, 2014) or hierarchical from non-hierarchical processing (Bornkessel-Schlesewsky et al., 2015). The level of detail of these representations remains largely underspecified.

1.2. Sensitivity to syntactic structure during incremental processing

While neural studies have become increasingly tuned to fine-grained linguistic differences between sentence and phrase types (e.g. Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Shetreet et al., 2009; Westerlund et al., 2015), the relationship between detailed linguistic grammars and language comprehension remains controversial. On one view, the abstract hierarchical grammars that have been developed to explain offline judgments and typological patterns should also serve to explain online comprehension (Berwick & Weinberg, 1983; Bresnan & Kaplan, 1982; Lewis & Phillips, 2015; Miller & Chomsky, 1963; Steedman, 2000). This is the *competence hypothesis*

> an explanatory model of human language performance will incorporate a theoretically-justified representation of the native speaker's linguistic knowledge