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Linguistic structure as a guiding principle for human neuroscience

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1. Behavior guides discovery in neuroscience

Advances in **neuroethology** (see Glossary) have far-reaching impacts on the field of neuroscience because specialized behaviors provide strong scaffolding for the investigation of neurophysiological circuits and their algorithmic bases. The discovery and documentation of the neural circuitry underpinning barn owl auditory spatial localization is well-noted in this regard (Carr and Konishi, 1988, 1990). The barn owl's specialized behavior, including head turns and prey-striking patterns, guided the investigation of its neural circuitry, providing evidence for the frequency range of the circuit's peak sensitivity (Konishi, 1973), the independence of time and intensity processing (Takahashi et al., 1984), and the importance of the interaural time difference for azimuthal localization (Moiseff and Konishi, 1981).

Such ethological approaches to neuroscience are successful precisely because they exploit the detailed structure of species-typical behavior. This applies as much to common animal models as it does to the barn owl: Well-described behavioral responses, from freezing in mice to courtship song in songbirds, are foundational to neuroscience because the intricate structure of the behavior triangulates the affordances of the neural system. In other words, these behaviors are useful to neuroscience not because they are unique to particular species but because aspects of their internal structure, development, and/or elicitation conditions are quantitatively distinctive enough to produce strong and detailed hypotheses about the underlying neurophysiology. It is in this sense that neuroethology is the study of brain physiology grounded in the quantitative analysis of species-typical behavior (Ewert, 1980).

We propose that the structure of human language enables this same kind of neuroethological approach and thus holds the same potential for determining core biophysical substrates of cognition in the human brain. This is not only because the use of language is a specialized, species-typical behavior with high ethological validity, but also because many structural aspects of language—both properties of specific languages, such as ergativity in Basque or tone melodies in Mende, as well as broader typological generalizations derived therefrom—are already well-described, quantified, and formalized; this is the purview of the broad field of **linguistics**.

However, where many linguists view theories as providing mental models of Language Knowledge, this Perspectives article privileges a view of linguistics in which theories provide candidate models of language structure, that is, models of licit language behavioral output (sign, speech), that are computationally explicit but mentally agnostic. We see this as a difference of lens on the theoretical objects at hand, one that centers a view of language as a physical, quantifiable behavioral signal, constituted by signs for signed languages and speech for spoken languages. In pointing to the importance of measurable linguistic 'read-outs,' we do not deny the importance of understanding Language as a mental phenomenon, nor do we advocate for explanations in linguistics, psycholinguistics, or neuroscience that are devoid of cognitive abstractions, representations, processes, or mechanisms. Rather, our motivation in adopting a surface-first lens is to show that linguistics already offers quantitative, and often formal, analyses of language necessary to readily advance both human neuroscience and the study of human cognition by offering key handholds on species-typical behavior and the neural

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activity that underpins it. That is, by leveraging the structure of language to understand neural substrates, we may have a better chance at inferring, studying, and reasoning about the cognitive mental representations, processes, and mechanisms that give rise to it.

As illustrated in Fig. 1B, a system of delay lines can be used to model sound localization (Jeffress, 1948). One strength of this model is its ability to account for interaural time difference effects in barn owl prey-striking behavior, a behavioral detail which Carr and Konishi exploited to substantiate the neurophysiological relevance of this model (Carr and Konishi, 1988, 1990). In this sense, the detail of the behavior narrowed the range of models entertained to account for it which in turn honed physiological investigation of the behavior's neural bases.

For a neuroethology of language, linguistics already supplies detailed documentation of language output and explanatory quantitative models of that output, as illustrated in Fig. 1A. English speakers can entertain two possible readings of the phrase *pink dog mug*. In one case, *pink* modifies *dog mug*, and in the other, it modifies *dog* alone. A difference in constituent structure, represented using a tree diagram in Fig. 1A, provides part of an explanatory account of the difference between these two English phrases, as explained further in Section 2.1. Thus, what barn owl striking behavior and the Jeffress model were for avian azimuthal auditory localization, structured and predictable use of language and models capable of accounting for those linguistic data are to human cognition.

Although we focus on constituency, many foundational properties of language phonetics, phonology, morphology, syntax, semantics, and pragmatics are sufficiently well-documented and extensively modeled to facilitate an approach from this perspective. That is, the descriptive groundwork for a human discovery as remarkable as that of the circuitry underlying barn owl auditory spatial localization is much in place.

In this article we illustrate the strengths of applying a neuroethological perspective to humans via human language using **constituency** as an illustrative example. We advance the position that explaining details of language structure, such as those central to the complexity of constituency, are critical to human neuroscience. We discuss the basic principles of constituency and provide examples of advantages this structure provides for the study of the human brain. We call for systematic studies to establish explanatory neurophysiological accounts of this kind of structure, and we discuss why language structure is a guiding principle for human neuroethology.

2. Case Study

2.1. *Constituency as a case study in how minimal assumptions reveal complex structure in language*

The intuition that some words within utterances are more closely related to one another than to other words lies at the core of syntactic theory. Consider the sentence in (1).

(1) Ames admires Reese's confidence.

English speakers tacitly know that *Reese's* is more closely related to *confidence* than other words in the sentence because it modifies the meaning of *confidence* but doesn't affect the meaning of *Ames* or *admires*. This intuition holds regardless of the predictability of the words involved. Linguists call this kind of relatedness constituency (Bloomfield, 1933; Chomsky, 1957), though cf. **dependency** (Mel'čuk, 1988; Tesnière, 1959). To determine which sets of words form constituents, linguists use various **constituency tests**, and when these tests are performed exhaustively on a sentence, a larger structure of nested constituents emerges (Fig. 2A). For many types of sentences, particularly in languages for which word ordering is relatively fixed, the **hierarchy** formed through exhaustive constituency testing will contain purely continuous constituents. This is true of the English sentence in Fig. 2. However, in many languages, including English, discontinuous constituents are also possible.

Discontinuous constituents occur when words or phrases that form a constituent are interrupted by those from another constituent (Bunt, 2012). They appear in a wide variety of genetically diverse languages and may occur due to topicalization, wh-fronting, scrambling, extraposition, or parentheticals (Bunt et al., 1987; Kariaeva, 2009; Louagie and Verstraete, 2016; Ojeda and Huck, 2020; Reinholtz, 1999). They tend to occur more commonly in languages with greater word order flexibility, such as German, Japanese, or Nahuatl, and different kinds of discontinuities can be more or less common in different languages. Sentence (2) provides an example of discontinuous constituency due to topicalization in English, where the subject (I) comes between the more closely related verb (don't like) and object (that idea).

(2) That idea, I don't like.

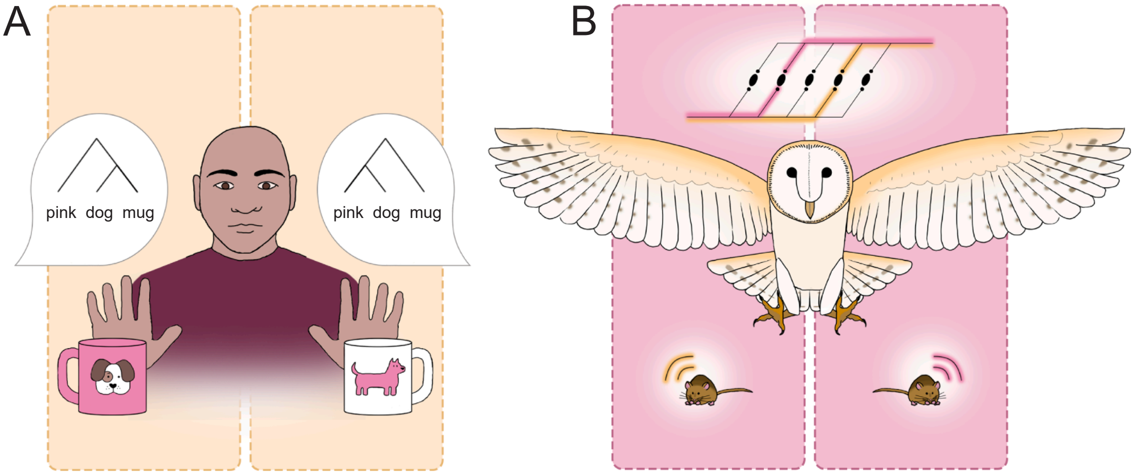

Fig. 1. The structure of behaviors provides evidence for the structure of the underlying neural substrate. **A.** Constituency provides an explanatory account for the difference in meanings associated with the situations in the left and right yellow panels: if *dog* and *mug* are more closely related than *pink* and *dog*, the mug on the left is chosen. Any account of language, including neural accounts, must be capable of accurately accounting for the unreasonable effectiveness of the mathematics of constituency to explain language behavior. This constraint limits the set of theories that can be entertained, providing focus and leverage for avenues of research. **B.** The auditorily-guided hunting behavior of barn owls constrained the sets of theories entertained for their auditory localization abilities. These observations were consistent with the theory that sets of neural delay lines and coincidence detectors could transform inter-aural differences in the timing of sounds into a spatial code (Jeffress, 1948). This model was substantiated using the predicted underlying structure of the behavior (=Jeffress' model) to guide the investigation (Carr and Konishi, 1988, 1990).

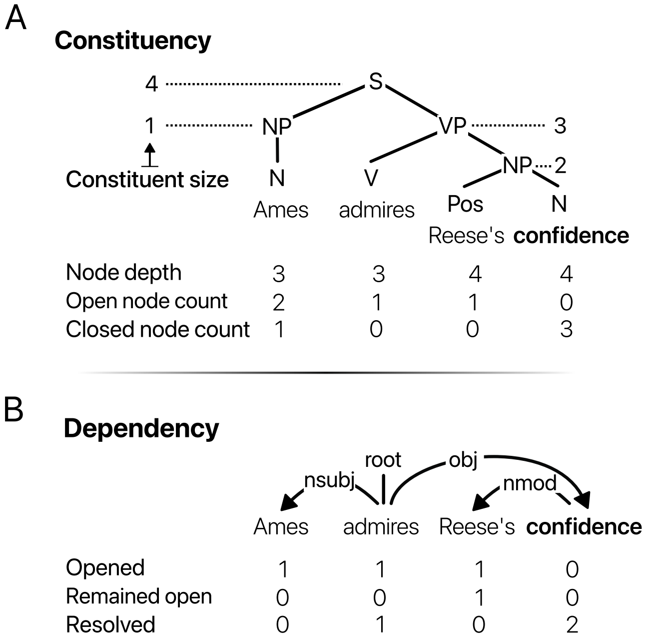

Fig. 2. Different theories of relatedness structure lead to different proposals for abstract structure. **A.** A tree diagram of the sentence "Ames admires Reese's confidence" represents its constituent structure at the word level. Constituent size, node depth, open node count, and closed node count can each be read from this diagram. **B.** A dependency parse of the same sentence yields a similar yet distinct structure. Below the parse diagram are counts of which dependencies have opened, remained open, and resolved as the sentence unfolds.

Prima facie, discontinuous constituents violate the assumption that closely related words and phrases ought to be linearly close to one another. Transformational theories of syntax, including Government and Binding Theory (Chomsky, 1981, 1982, 1986) and the Minimalist Program (Chomsky, 2014), rescue this assumption by positing an abstract underlying structure with continuous constituents that undergoes structured transformation to arrive at the sentence with discontinuous constituents that is produced. For a sentence like (2), this means that the underlying structure originates as the structure for "I don't like that idea" and undergoes a transformation that 'moves' the noun phrase *that idea* to the left edge of the structure. On the other hand, traditional dependency-based theories of syntax reject this assumption and prioritize the hierarchy that constituents create, which is unaffected by linear discontinuity (Mel'čuk, 1988; Tesnière, 1959). More concretely, for a sentence like (2), the dependency between the noun phrase *that idea* and the verb *like* remains that of an object depending on a verb, regardless of whether *that idea* comes before or after the verb.

The theoretical complexities raised by discontinuous constituents highlight two key strengths of using linguistic structure to guide neuroethological investigation. First, slight differences in foundational assumptions can lead to the development of substantially different models of language structure. Even a seemingly innocuous assumption, such as that mentioned above, can have significant downstream consequences, and small differences in assumptions can proliferate computationally distinct offshoot theories. On the one hand, this leads to a diverse array of extant theories, but on the other, it provides a well-populated space of detailed hypotheses for investigation. Second, language diversity challenges these hypotheses to be cross-linguistically robust. If a neural signature specific to scrambling is observed in speakers of German, we may expect to observe it in speakers of other scrambling languages, such as Dutch and Japanese as well. Inversely, we may also expect not to observe it in speakers of non-scrambling languages, such as English. In this way, language diversity enables rigor in hypothesis testing and raises standards of evidence in the neurobiology of language.

Even setting aside theory-specific assumptions, the basic structure of constituent hierarchy holds non-trivial linguistic information. Purely continuous constituency hierarchies can be modeled using an abstract formal structure called a **context free grammar** (CFG) (Chomsky and Schützenberger, 1959), and without the imposition of theory-specific abstract structure, the properties of linguistic CFGs are distinct from those of non-linguistic CFGs (cf. Linear Context-Free Rewriting Systems (Vijay-Shanker et al., 1987) or Tree-Substitution Grammars (Bod, 2008; Joshi et al., 1975) for discontinuous constituents). This is because linguistic constituency is non-random. In probabilistic CFGs, when the number of non-terminal symbols and degree of determinism in rule application are varied, a relatively narrow range of these parameter values result in grammars that produce strings functionally distinguishable from random sequences (DeGiuli, 2019a, 2019b). That is, even among hierarchical structures produced by CFGs, those that are language-like represent only a fraction of possible grammars. This points to the high degree of information latent even in the simplest representations of linguistic hierarchy and underscores the potential for basic linguistic observations to provide meaningful signatures of the kinds of information that must be available in brain activity during language processing.

Neuroimaging substantiates this potential, using measures of **constituent size**, **node depth**, **open node count**, and **closed node count** derived from sentential tree structures to quantify the linear, sequential constituent structure alongside its nonlinear, hierarchical depth. Sensitivity to these measures of constituent structure has been observed intracranially for English and French speakers (Nelson et al., 2017) as well as non-invasively in French Sign Language (LSF) users (Moreno et al., 2018) and Dutch, English, Mandarin, and French speakers (Bai et al., 2022; Brennan et al., 2016; Coopmans et al., 2025; Ding et al., 2016; Pallier et al., 2011; Zioga et al., 2023), and left superior temporal sulcus, inferior frontal gyrus, and left basal ganglia appear most involved in the processing of these constituency measures during reading (Moreno et al., 2018; Pallier et al., 2011). Thus, neural activity appears in part to reflect both the linear and hierarchical organization of constituents.

However, as much as these results demonstrate the efficacy of constituency to explain language-related brain data, they also highlight what remains unknown: the underlying mechanisms responsible. This is where a neuroethological approach to language becomes instrumental. Rather than identifying features of language that explain variance in the neural signal, a neuroethological approach asks how the structure and operations of the brain could support the patterns observed in language. This shift in approach brings a shift in perspective more than a shift in methods. For constituency, whole-brain recordings that demonstrate the sensitivity of the brain to metrics of linear and hierarchical structure set the stage for investigation of systems-level mechanisms. With current neuroimaging technology capable of observing single-cell (Leonard et al., 2023) and cerebral columnar representations (Lage-Castellanos et al., 2023), that is, at scales commensurate with those of barn owl auditory spatial localization, neuroethological approaches to language stand poised to uncover cellular- and circuit-level mechanisms as well.

2.2. *Constituency as case study in how complex structure can be used to probe underlying neural mechanisms*

Constituent structure is a widespread feature of language, yields clear quantitative measures of structure, and has been shown to explain some of the neural response to sign and speech. These properties make it a prime target for narrower investigation of the neurophysiological bases for language.

At the cellular level, techniques for the estimation of receptive fields such as spatio-temporal receptive fields (STRF) (Theunissen et al., 2000, 2001), maximally informative dimensions (MID) (Sharpee et al., 2004), or maximum noise entropy (MNE) (Fitzgerald et al., 2011a,b), could be used to characterize whether putative individual neurons track constituent structure. Each of these models posits a different function between stimulus features and response properties, thereby offering different hypotheses for the stimulus-response relationship. For example, STRFs posit a linear relationship between stimulus and response, while MNE models accommodate higher-order quadratic relationships. Fitting receptive field estimation models using abstract features of constituent structure, such as node closure count, therefore tests specific hypotheses about the relationship between constituent structure and neural activity. In this way, receptive field estimation techniques may help advance understanding of the transformations that linguistic information undergoes in single units.

Exploitation of features like node closure count could also be used to determine whether constituency is supported by circuit-level dynamics. Local field power in the high gamma band changes in a temporally precise, step-up and step-down manner time-locked to changes in node closure count (Nelson et al., 2017). Lower-level mechanisms for this neural signature are currently unknown, but encoding strategies employed in other aspects of the brain response to language may help build testable theories. For example, sites characterized as having onset or sustained responses to acoustic properties of speech have been consistently found throughout superior temporal gyrus (Hamilton et al., 2018). If sites with onset and sustained response properties were sensitive to features of constituent structure, it could be tested whether the coordination of activity across onset and sustained sites could result in the kinds of local field power changes previously observed. This kind of approach illustrates how testing for sensitivity to linguistic structure across multiple scales of analysis can help build theory that connects how language is processed throughout the brain.

At the systems level, constituency may draw on the properties of oscillations as representations of aspects of sensory information. If the phase of oscillations recorded in key areas for language processing synchronizes when constituent nodes open or close, as shown by Weissbart and Martin (2024), constituent structure could be the consequence of distributed synchronous activity coordinated by oscillatory phase. This would also be consistent with work showing that oscillatory phase coordinates synchronous population activity (Lisman and Jensen, 2013; Mehta et al., 2002; Schaefer et al., 2006) and that phase impacts language processing differently in different language-related regions (Ten Oever et al., 2024). Alternatively, spike timing relative to oscillatory phase could encode features such as node depth, or the relative number of open nodes. This mode of representation would resonate with the observation that phase synchronization to the onset of phrasal constituents can be experimentally induced (Ding et al., 2016).

Rather than representing stimulus features *per se*, oscillations may also function as regulators of information flow (Akam and Kullmann, 2010; Colgin et al., 2009; Hillebrand et al., 2016; Sejnowski and Paulsen, 2006). This hypothesized role for oscillations also derives from their ability to temporally coordinate spiking activity. The firing of a particular neuron depends not only on the number of inputs that fire upon it, but also on their coincidence relative to one another. Thus, to the extent that oscillations enforce more stable regimes for coincident activity to occur, they can regulate the signal-to-noise ratio of select spiking activity relative to background. Seen in this light, the behavioral insight at the core of constituency—language users' intuition that some words are more closely related to one another than others—could derive from modulation of the gain of neuronal integration (Martin, 2020). That is, the strength of constituent membership could be modulated by the extent to which oscillations facilitate coincident activity that binds groups of words into constituents or sets of constituents into larger constituents (see Martin and Doumas, 2017 for a computational model).

These proposals are necessarily speculative, yet testable and refinable. They exemplify not only the potential of a neuroethological approach guided by linguistic structure to deepen explanation of language, but also the achievability of such progress. Language-related single unit recordings will likely remain uncommon relative to less invasive neuroimaging methods, but many of these proposals are testable using non-invasive techniques and/or pre-existing datasets as well.

2.3. Going beyond constituency: consequences of language structure for human neuroethology

We have argued that linguistic structure provides a strong basis for investigation of the brain basis of language. In particular, we have shown that constituency, a simple and foundational property of language organization, has sufficiently idiosyncratic structure to identify neural activity specific to linguistic, structure-building processes and to restrict the set of hypotheses linking linguistic structure to neural substrate.

Constituency plays a central role in several influential proposals for language evolution. Notably, it has been argued that recursion, integral for the generation of constituent structure, is the core component of the human faculty for language (Hauser et al., 2002). Similarly, it has been asserted that the compositional rules that enable humans to "attach discrete symbols to mental representations and to combine those symbols into nested recursive structures" are foundational to linguistic cognition and what distinguishes human cognition from that of other animals (Dehaene et al., 2022). It is also argued that the "propensity by our species to infer tree structures from sequential data" sets humans at the extreme of this axis of cognitive ability (Fitch, 2014). In this sense, the typicality of constituency within human behavior is well recognized.

However, the hypothesized importance of constituency for language evolution in itself is not what makes constituency a prime candidate for unlocking the neural substrate for language. Its relevance to language evolution may make it more likely to have dedicated or specialized biophysical foundations, but the intricacy and specificity of its structure are what give it a practical edge—that is, the ability to generate experimentally testable hypotheses as intricate and specific as the structure itself. This advantage holds for all properties of language structure and organization: structural and organizational properties such as the behavior of phonological natural classes, (morpho)phonological alternations, morphological agreement, the logical properties of conjunctions and quantifiers, and more. Each of these phenomena bears its own distinctive quantifiable structure, and thus in turn offers a wide array of possibilities for structured neuroethological investigation.

Linguistic structure has unique purchase on the biophysical substrate of language and in turn on key dimensions of brain computation because linguistic behavior spans the range of what neural systems do: they develop and maintain sensitivity to abstract features of their environment relevant for specific behaviors; they maintain information pertinent to the statistical dynamics of both first-order sensory input and higher-order abstract learnable categories; and their learned categories exhibit great robustness to noise, yet they conserve the ability to alter and construct new categories over the lifespan. All of these properties make language indispensable to human neuroscience.

Moreover, beyond simply spanning the range of what neural systems do, some aspects of the biophysical substrate of language are likely linked with those of other cognitive faculties. As one example, working memory demands are implicated in the processes required to develop and maintain syntactic long distance dependencies (Ferrer-i-Cancho, 2004; Futrell et al., 2015, 2020; Gibson, 1998, 2000; Hawkins, 1994; Liu et al., 2022; McElree, 2006; Temperley and Gildea, 2018). Consequently, leveraging a neuroethological approach to the study of syntactic long distance dependencies has the potential to meaningfully advance understanding of aspects of working memory as well. In this sense, the brain basis of language has concrete implications for mechanisms fundamental to other human cognitive faculties.

Alongside its boundary-condition–spanning computational properties and rich connections with other cognitive domains, human language offers quantifiable behavioral readouts in the form of produced sign and speech and what is comprehended therefrom. Linguistic research continues to deliver formal and quantified theories about the structure and statistics of sign and speech that can be leveraged to discover the neural mechanisms underpinning these behaviors. Thus, the scientific challenge is to effectively transduce the core ethological observations of those theories into neuroscientifically meaningful coordinate systems (Embick and Poeppel, 2006, 2015; Martin, 2016, 2020), enabling linguistic and neuroscientific models and theories to have intertranslatable explanatory force in both domains (Guest, 2023; Guest and Martin, 2021, 2023).

3. Concluding Remarks

Here we have focused on a single property of linguistic structure that we believe illustrates the great promise of language structure for neuroscience as a whole. We have shown that constituency is a core property of language that differs non-trivially from other grouping relationships, and we have described how it scaffolds lexical grouping structure. We have identified existing literature that points to the significance of constituency to the neural response to sign and speech, and we have sketched ways that constituency can be further leveraged to investigate language responses at cellular, circuits, and systems levels of organization. Altogether, this work advances the position that taking an ethological approach to language and its structure has the potential to push human neuroscience forward at multiple scales of investigation.

At the same time, it is not our goal to argue that language ought to be privileged above other distinctive human cognitive abilities and behaviors, such as those involved in music or mathematics. Insights from theories of music, mathematics, and other highly structured human abilities may also provide valuable purchase on the discovery of mechanisms fundamental to human cognition. From the model this Perspectives article provides, outlining the value of bringing linguistic theory into neuroscientific inquiry from a neuroethological perspective, we encourage the development of complementary proposals for other domains of cognition and behavior as well.

In the past, auditory research has taken inspiration from vision (Rauschecker, 1998), and this has in turn generated numerous productive lines of neurolinguistic research (Bornkessel-Schlesewsky et al., 2015; Brennan, 2022; Hagoort and Indefrey, 2014; Hickok and Poeppel, 2007; Poeppel and Assaneo, 2020; Pylkkänen, 2019). However, more recent work complicates the analogy of language processing pathways to visual processing pathways (e.g., Hamilton et al., 2021). We hope that in encouraging further research that capitalizes on the ethology of language and its quantifiable properties, results in the neurobiology of language will similarly inspire theory and research approaches in other areas of neuroscience.

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Declaration of Interests

The authors have no competing interests to declare.

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Glossary

Constituency: A view of linguistic relatedness structure that focuses on part-whole relationships in sentences, such that each element (i.e., word, morpheme) in a sentence may correspond to one or more nodes in the underlying syntactic structure.

Constituency test: Sentence manipulations designed to determine whether a string of words functions as a unit (constituent). Tests include substitution of the string with a pro-form like “it” or “there”, topicalization of the string by moving it to the front if the sentence, clefting of the string into the form “it is/was _ that…”, or coordination of the string with another similarly structured string. If these manipulations yield acceptable utterances, the proposed unit is likely a constituent. For example, in Fig. 2, “Reese’s confidence” can be successfully clefted (It is Reese’s confidence that Ames admires), but “admires Reese’s” cannot (*It was admires Reese’s that Ames confidence). This indicates that “Reese’s confidence” is a constituent but not “admires Reese’s”.

Constituent size: A measure of the number of words or morphemes in each constituent.

Context-free Grammar (CFG): A class of formal grammar comprising rules of the form $A \rightarrow \alpha$, where A represents non-terminal elements, and α represents a non-empty string of terminal and/or non-terminal elements. For example, the sentence in Fig. 2 could be generated by the set of rules given here: 1. S → NP VP, 2. NP → N, 3. VP → V NP, 4. NP → Pos N.

Dependency: A view of linguistic relatedness structure that focuses on part-part relationships in sentences, such that each element in a sentence depends on at most one other element.

Hierarchy: A kind of relationship structure in which each element is directly subordinate to at most one other element.

Linguistics: The scientific study of language and its structure. This involves study of particular languages, both signed and spoken, and the analysis of their phonetics, phonology, morphology, syntax, semantics, and pragmatics.

Neuroethology: The study of brain physiology grounded in the quantitative analysis of species-typical behavior.

Node closure count: A measure of how many constituents end (close) at each word.

Node depth: A measure of vertical distance within a tree-like syntactic structure, counting the number of nodes from the root node to the current node.

Open node count: A measure of how many constituents begin (open) at each word.