REVIEW

The neural basis of combinatory syntax and semantics

Liina Pylkkänen[1,2]

Human language allows us to create an infinitude of ideas from a finite set of basic building blocks. What is the neurobiology of this combinatory system? Research has begun to dissect the neural basis of natural language syntax and semantics by analyzing the basics of meaning composition, such as two-word phrases. This work has revealed a system of composition that involves rapidly peaking activity in the left anterior temporal lobe and later engagement of the medial prefrontal cortex. Both brain regions show evidence of shared processing between comprehension and production, as well as between spoken and signed language. Both appear to compute meaning, not syntactic structure. This Review discusses how language builds meaning and lays out directions for future neurobiological research on the combinatory system.

When exposed to a familiar language, our brains automatically compose the individual words together into larger meanings. Even without language input, our brains do something similar: We create new meanings in our thoughts and even comprehend our own creations. This is the internal "chatter" that, for most humans, is hard to shut down. Although combining meanings is instinctive and automatic, our minds actually perform some rather complex mental gymnastics while doing so. Consider these seemingly simple sentences:

Sally baked the black beans.
Sally baked the beans black.

In the first sentence, black describes a property of the beans prior to the baking, a so-called modifier reading. In the second, the blackness of the beans is caused by the baking, a resultative reading. We can even make the meaning ambiguous by adding a modifier to the adjective itself:

Sally baked some beans black enough to look like licorice.

In this sentence, Sally could either be baking beans that have a licorice-like appearance (modifier reading) or she could be baking beans until they turned as black as licorice (resultative reading).

Our brains make these distinctions on the basis of syntax. The example sentences illustrate three structures allowed by the syntax of English: prenominal modification (adjective before noun), resultative secondary predication (adjective follows the noun and describes a resultant state of the main "primary" predicate, the verb), and postnominal modification, which is semantically equivalent to prenominal modification but is only grammatical when the modifier satisfies certain length and/or weight requirements. Your brain has long-term memory traces corresponding to these structures and is therefore able to evaluate incoming language against this knowledge. This much is uncontroversial. But what are the online computations that serve to merge or combine words during language processing, such that the relationship between the composed representations and our knowledge of syntax can be evaluated? This Review focuses on our current understanding of this question.

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Comprehension: Rapid concept composition in the left anterior temporal cortex

Just as biologists prefer to study small animals with fewer cells when trying to understand living organisms mechanistically, it has proven productive to start simple in the neurobiology of meaning composition as well. When it comes to brain mechanisms of language, a full sentence is like an elephant. A short, two-word phrase is a more tractable representational unit, and thus research has begun to characterize the composition of these minimal phrases (*1*–*10*) (Fig. 1). The goal is to functionally decompose a perisylvian brain network implicated for the processing of full sentences (*11*).

When we understand language, dozens of processing stages are packed into a few hundred milliseconds. For this reason, detailed time resolution is an important requirement for our measurement device. This Review focuses on research that has used magnetoencephalography (MEG), the only noninvasive technique that offers both the millisecond resolution required for characterization of rapid language processing as well as reasonably accurate spatial localization of the neural currents generating the measured signals. Neuroscience techniques that track blood flow, such as functional magnetic resonance imaging (fMRI) or positron emission tomography, have good spatial accuracy but are too slow to characterize the time course of rapidly unfolding language.

Although a two-word phrase is simpler than a sentence, its composition still likely engages many different types of combinatory routines (Fig. 2). For example, to account for the syntactic and semantic behavior of a simple phrase such as "black cat," linguistics and cognitive psychology hypothesize at least three types of structures: (i) the syntax, in which the categories "noun" and "adjective" join to form a noun phrase (*12*); (ii) the logical semantics, in which the properties of blackness and catness intersect to yield a representation of entities that possess both properties (*13*); and (iii) the conceptual structure, in which the features of the two concepts combine (*14*). Because these representations may be built simultaneously in parallel, a problem for a mechanistic understanding of composition is to determine whether these possibly distinct representations dissociate in neural activity.

First, we need a characterization of what happens in the brain when a person hears or reads a word in a minimal combinatory context. Most studies on minimal phrases have used adjective–noun combinations. Results show that in English, this type of basic composition increases activity in the left anterior temporal lobe (LATL) at 200 to 250 ms after noun onset, as compared with the processing of the same noun in a context in which it cannot combine with the preceding word (*1*, *2*). If the language has the reverse word order, noun before adjective, the same result is seen with respect to the processing of the adjective (*6*). About 200 ms later, another activity increase often occurs in the ventromedial prefrontal cortex (vmPFC) (Fig. 1). What aspects of composition do these neural traces reflect?

Syntactic effects are difficult to distinguish from semantic effects, because in natural language, syntactic changes usually alter the meaning of the expression. Consequently, many results on the neural basis of basic syntactic composition are actually results on the processing of artificial stimuli that are intended to lack meaning. Most commonly, such expressions are made up of nonsense words strung together with real affixes and other grammatical vocabulary (*4*, *5*, *8*, *15*–*17*). Processing such stimuli may substantially differ from the comprehension of natural language.

Whereas syntax is difficult to vary while keeping meaning constant, the reverse is easier: It is possible to keep syntactic structures constant while varying meaning. In fact, such manipulations have ruled out a syntactic explanation for both the left temporal and ventromedial combinatory effects when measured with MEG. The LATL's early (200 to 250 ms) contribution to composition appears conceptual in nature. This finding is consistent with those of hemodynamic and neuropsychological studies (*14*, *18*).

Within the two-word paradigm, as used in MEG, the clearest evidence for the conceptual hypothesis comes from studies that have manipulated the conceptual specificity of the combining lexical items. LATL amplitudes elicited by the second word of a phrase appear to reflect the proportion of features contributed by the first word onto the combined feature set of the whole phrase (*7*, *9*). Consider the phrase "Indian food." Here, the modifier "Indian" restricts the set of foods to which the noun refers: all cuisines apart from Indian are excluded. The modifier "Asian" would have a weaker effect, because "Asian food" may refer to any type of Asian food (Korean, Japanese, Indian, etc.). This is the type of factor to which the LATL is sensitive (Fig. 2) (*9*). As the feature space of the first word becomes more specific, the magnitude of the observed LATL signal increases when that word is integrated onto the second word. The feature space of the second word matters as well: the vaguer the meaning, the more the first word affects the joint feature set of the whole phrase and the larger the observed LATL signal on the second word (*7*). Neither the syntactic nor the logico-semantic system has any representation of the conceptual feature space in these terms, and thus neither system can explain these patterns. Studies also reveal that the LATL can operate in the absence of local syntactic combination, as long as the task goal is to combine meanings (*2*, *19*).

If the LATL combines some aspects of word meanings at 200 to 250 ms, those aspects must have been retrieved from memory by that time. This estimate is on the early side, given that classic and widely replicated findings about the timing of semantic access place it at 300 to 400 ms (*20*). However, today we also have evidence that semantic access can begin much more quickly—as early as the 100-ms mark (*21*, *22*). The semantic feature space may activate gradually in a few hundred milliseconds (*23*), by some yet-to-be articulated mechanism.

The hypothesis space regarding vmPFC function is still very open, although we do know that the vmPFC is also sensitive to semantics within syntactically parallel expressions. Therefore, it also is unlikely to reflect syntactic aspects of composition. The evidence for this comes from the processing of expressions that involve implicit meanings triggered by semantic mismatches within well-formed expressions (*24*). Overall, the results conform to a model in which the LATL serves as a rapid nonsyntactic feature combiner (*25*) and the vmPFC contributes to a late stage of composition, perhaps representing the final output of the entire combinatory processing stream in a region connected to broader systems of social cognition and episodic memory (*26*).

Note, however, that this account does not address other possible contributions of these regions. The LATL, for example, also participates in the processing of single words. This suggests that the region not only binds features across words but also connects features that make up

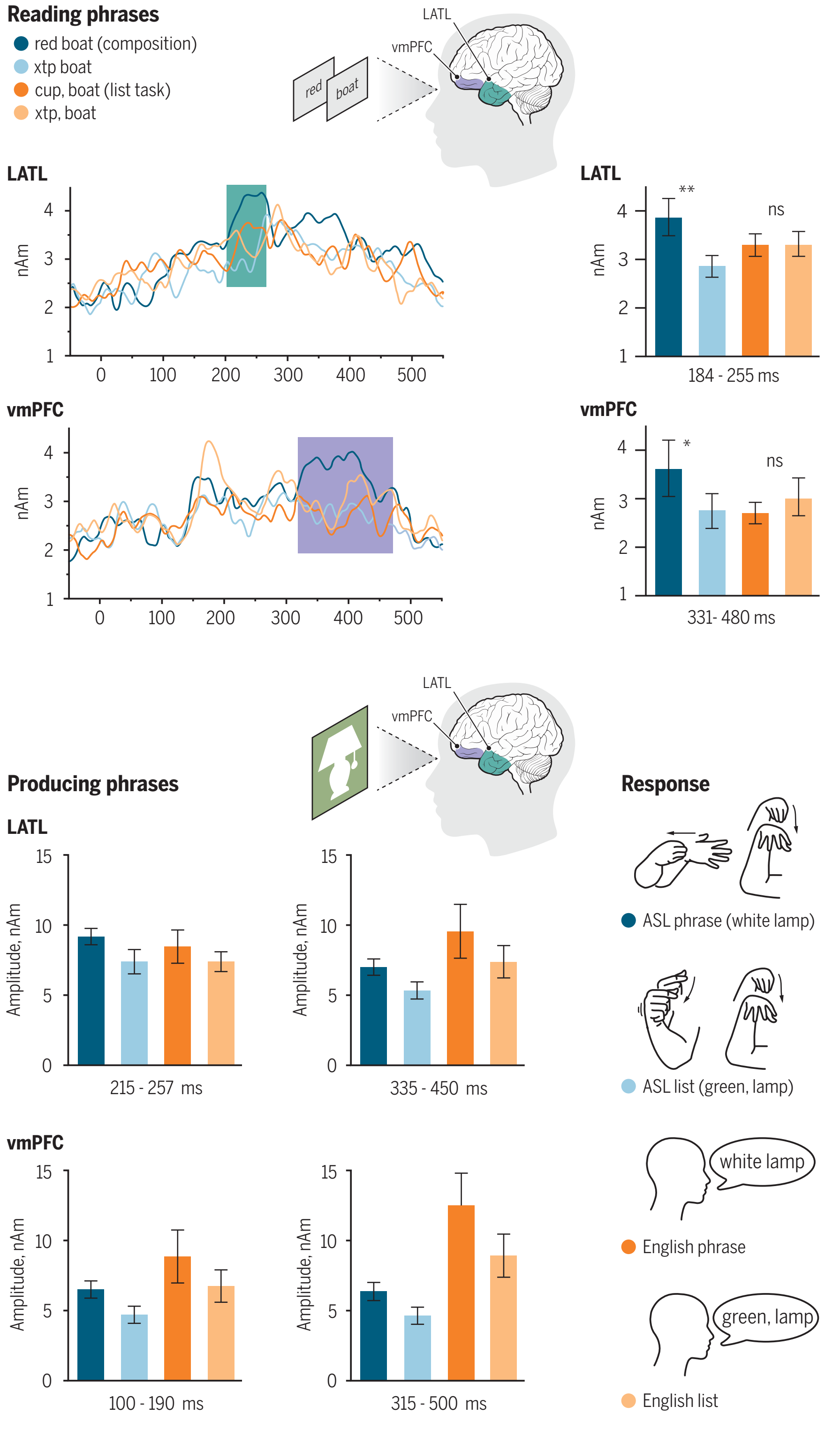

Fig. 1. Building phrases in comprehension and production. A single step of composition engages the LATL and vmPFC. In comprehension (top), LATL engagement precedes vmPFC engagement (*1*), but in production (bottom) the two operate in more parallel fashion. In production, a picture-naming paradigm allows for the study of different languages while controlling the physical stimulus perfectly. One can simply ask participants to name the pictures in different languages. Here, similar LATL and vmPFC effects are shown for the planning of phrases in English and American Sign Language (ASL) (*3*). Recent research has addressed the functional roles of these neural signatures of composition, demonstrating that neither appears syntactic in nature and that the LATL has a distinctly conceptual profile (*7*, *9*, *24*, *25*). nAm, nanoamperes. Error bars indicate SE. $^*P < 0.05$; $^{**}P < 0.01$; ns, not significant.

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single concepts [e.g., their visual appearance, function, or size (*18*)]. In MEG, activity reflecting across-words binding (composition) is more robust than activity reflecting within-word binding (word retrieval) (*7*, *9*), perhaps because the former creates a new meaning whereas the latter activates an existing connection.

But here is a puzzle: If the LATL is damaged, single-word processing is impaired, not phrase composition (*27*, *28*). How could this be if the LATL is a combinatory hub? A possible answer lies in the redundant nature of the combinatory system, as depicted in Fig. 2. If many different subroutines carry a roughly similar function (i.e., building a phrase), then this system may be difficult to break. The function of an impaired subroutine could be compensated for by the others, at least to some degree. In contrast, feature binding within a word may not have similar redundancy. This would make single-word processing more fragile than basic combinatory processing. Indeed, focal brain damage hardly ever results in the inability to form simple phrases, whereas problems in single-word access and more-complex syntactic processing are classic patient profiles.

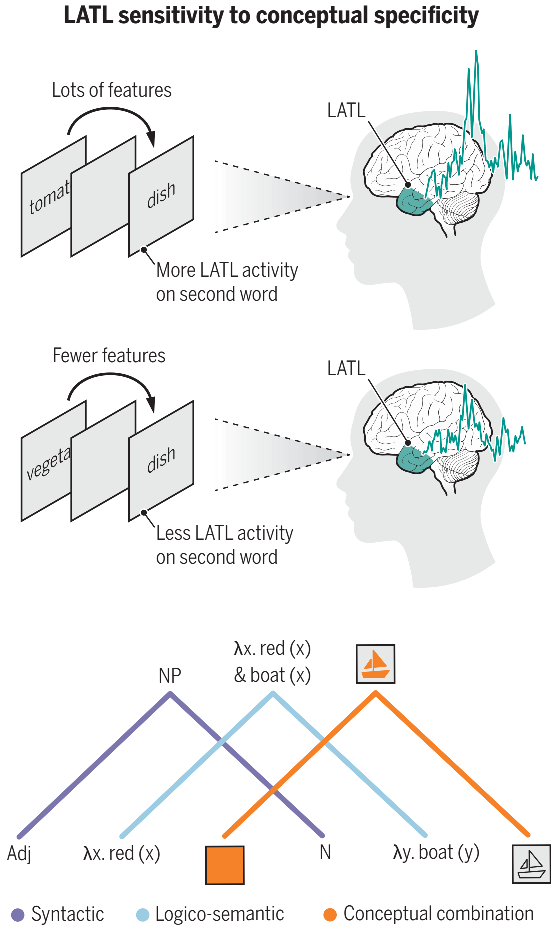

Fig. 2. Components of composition and conceptual sensitivity of the LATL. Composition is thought to subdivide into syntactic, logico-semantic, and conceptual subroutines. The LATL shows a larger signal when a more specific meaning integrates into a word from context and is therefore unlikely to reflect syntactic or logico-semantic aspects of composition (*7*, *9*). NP, noun phrase; Adj, adjective; N, noun.

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Production: Planning phrases in speech and sign

Although the terms "speech" and "language" are often used interchangeably, speech is only one way to externalize language, as indicated by the use of more than 200 signed languages around the world. Signed languages allow for tests about whether a result reflects the fundamental core of human language or relates to the specifics of spoken languages. In general, signed and spoken languages are known to be fundamentally similar systems (*29*) and engage the same broad brain networks (*30*). However, understanding is more elusive for more-specific processes. For the minimal composition results discussed above, we have evidence for similarity between spoken and signed language. Detecting such similarity is difficult in comprehension, because the nature of the physical signal differs markedly for the two types of languages. At the earliest stages of perception, hand movements and sounds engage entirely different systems, which makes the detection of similarity methodologically challenging. However, the early planning stages of language production could be very similar until the planned representations begin to engage the motor systems, as shown in a study that used picture naming as a shared production task for speakers of English and for congenitally deaf signers of American Sign Language (*3*).

In this picture-naming study, both speakers and signers named colored objects with adjective–noun combinations, such as "blue cup." Thus, the physical stimuli (the pictures) were identical for the two groups. Bringing added value, the noncombinatory control condition was lexically matched to the combinatory condition by presenting the colored object on a colored background (for example, a blue cup on a red background) and instructing participants to name the background color and the object during the noncombinatory trials. Participants produced adjective–noun sequences in both conditions, but only in one did the words form a coherent combinatory representation. Replicating prior findings for English, the study showed that both signers and speakers engaged the LATL and vmPFC while planning the phrases describing the colored objects but not while planning the background color–plus–object descriptions. Thus, neural reflections of composition manifest for both comprehension and production and also generalize to a different set of articulators.

Syntax: Where is it hiding?

Although the body of work discussed so far has delineated a starting point for understanding the brain's mechanisms for meaning composition, it seems to have taught us nothing about syntax. So far, each correlate of composition has turned out to be semantically sensitive. The neuroscience-of-language field has long assumed that our brains build syntactic structure during language processing. Today, it is reasonable to question this assumption.

Is there a neurally implemented computation that builds syntactic structure and does not compute any meaning—a mechanism that, upon encountering "angry bird," composes the representation of the adjective category with the representation of the noun category to yield a representation of a noun phrase, with no information about the meanings of the elements that were combined?

Despite much published literature on the neural underpinnings of syntax and a lesser amount on the brain basis of semantic composition, the brain basis of syntactic composition remains mysterious (*25*, *31–34*).句法研究

The state of the art can be summarized as follows:

1) During the processing of natural, meaningful language, neural signals (as measured by currently available techniques) are dominated by correlates of meaning, not structure, in both the two-word paradigm (*25*) and full sentences (*31*). This does not mean that syntax is not also computed, but it does make the isolation of syntactic computations more challenging.

2) When brain activity associated with sentence processing is modeled, word by word, with measures of syntactic structure, the models reliably predict activity in several regions (*35–37*). However, we do not know the degree to which these results are driven by purely structural processing or by combinatory semantic processing. For each element of additional structure, an element of meaning is usually added as well. Teasing apart structure and meaning is the fundamental challenge for the study of composition in natural language.

3) When syntactic phrases are presented to listeners at consistent, predictable rates, electrophysiological responses show power increases that match the presentation rates of those structures, even in the absence of physical cues to structure (*38*). That is, our brains notice phrases. Is the brain rhythm tracking syntactic or semantic combinatorics? This

question is still open, but the rhythmic tracking has been replicated for an artificial grammar without meaning, pointing toward a purely structural origin (*39*). Next, we should ask whether these rhythms also track nonlinguistic chunking or grouping. Such tracking would suggest either that the rhythms reflect something more general than combinatory language operations or that combinatory operations in language share properties with general chunking processes. Regardless, these rhythms may be a clue to syntactic parsing during comprehension.

Understanding the broader combinatory network

What are the most fruitful research directions for future progress in our understanding of linguistic composition in the brain, especially with regard to syntax? Results suggesting that the LATL can combine concepts, even when they do not syntactically combine (*2*, *19*), indicate that, rather than trying to vary syntax while keeping meaning fully constant, we can aim to vary syntax in ways that should not affect activity in the LATL. To achieve this, we would vary syntax but not the string of conceptually informative items. Conditions may differ in some aspects of meaning but would pose similar opportunities for conceptual combination. Studies following this logic have found evidence for more structure-based processing in the left posterior temporal lobe (LPTL) (*19*, *40*). MEG measurements suggest that the timing of this activity parallels that of activity in the LATL, starting at ~200 ms (*11*, *16*, *19*). Thus, different parts of the temporal lobe may simultaneously compose different aspects of structure and meaning.

In addition to the LATL, vmPFC, and LPTL, at least two other regions are thought of as part of the broader combinatory network (*25*): the angular gyrus (AG) and the left inferior frontal gyrus (LIFG) (Fig. 3). In MEG measurements, the AG peaks sharply around 170 ms after the onset of a visual word and shows sensitivity to the number of argument slots the word has. For example, a transitive verb elicits higher activation than an intransitive one (*41*), replicating prior hemodynamic research (*42*). Given the robustness of the signal from this region, future work should be able to delineate how this region represents the combinatory potential of individual words.

The LIFG has been associated with syntactic combination in several prominent models (*43*, *44*), on the basis of both hemodynamic and patient data. However, this region has been relatively silent in MEG studies of composition (*1*, *16*, *35*). Consequently, the timing of this activity is not well understood, which has limited our ability to formulate specific functional hypotheses of this activity. However, a large-sample MEG study has identified a mid-latency timing for LIFG activation during sentence processing, at ~300 to 450 ms after word onset (*11*). This timing conforms to prior MEG results showing increased LIFG amplitudes for long-distance dependencies (as in relative clauses in which the object of a verb is expressed outside its canonical object position: e.g., "the ball that the dog ate") (*45*). This result replicates prior hemodynamic literature, starting with the classic study of Stromswold and colleagues (*46*). Thus, whereas the participation of the LIFG in long-distance dependencies receives support from multiple methods, the same is not true for basic composition. To understand the discrepancy, more studies are needed in which the same design is used with both MEG and fMRI (*16*).

Finally, controlled laboratory experiments should continue to be complemented with naturalistic experiments that analyze real-world comprehension of language, such as in stories or podcasts (*35*, *37*). In naturalistic studies, neural activity is modeled, word by word, by regressors that represent various properties of the stimuli, including their combinatory properties. Though powerful, this method is only as good as the accuracy of the employed regressors as representations of the modeled processes. We currently have a paucity of computational models of incremental semantic composition, as opposed to syntactic phrase building, and therefore this body of work has not addressed the syntax-versus-semantics question. More effort should be directed toward developing computational models of incremental semantic composition. Today, such models can be informed by our understanding of conceptual processing in the LATL—that is, we can create regressors designed to track LATL activity as it has been observed in controlled experiments.

Syntax as knowledge, semantics as process?

What if, after all of our efforts to find purely structural processing in the brain, we still find nothing? Syntax in the brain is necessary to explain the fact that humans are exquisitely skilled at judging syntactic well-formedness, even for sentences that have no coherent meaning. Chomsky made this point with his "colorless green ideas sleep furiously" example (*12*), which we recognize as a grammatical English sentence, although is it semantically incoherent. But what if we cannot find evidence that our brains actually build syntactic structure?

Syntax may be something that the brain knows rather than does. Perhaps the combinatory steps, which consume energy and make our neurons fire, are all semantic, and syntactic processing amounts to comparing these semantic structures to our stored knowledge of syntax. The knowledge may have the format of generative rules that create structure (*12*) or may represent the structures themselves (*47*). This type of "syntax as knowledge, semantics as process" model would make pure syntactic composition unmeasurable in the incremental combinatory steps that build sentences. However, syntactic knowledge could still be used to make predictions about upcoming language (*48*), and thus neural activity could be modulated by the degree to which the encountered language matches the predictions. These types of syntactic prediction effects have been widely documented both for behavioral (*49*) and neural measures (*50*). In summary, on this hypothesis, top-down predictions could be

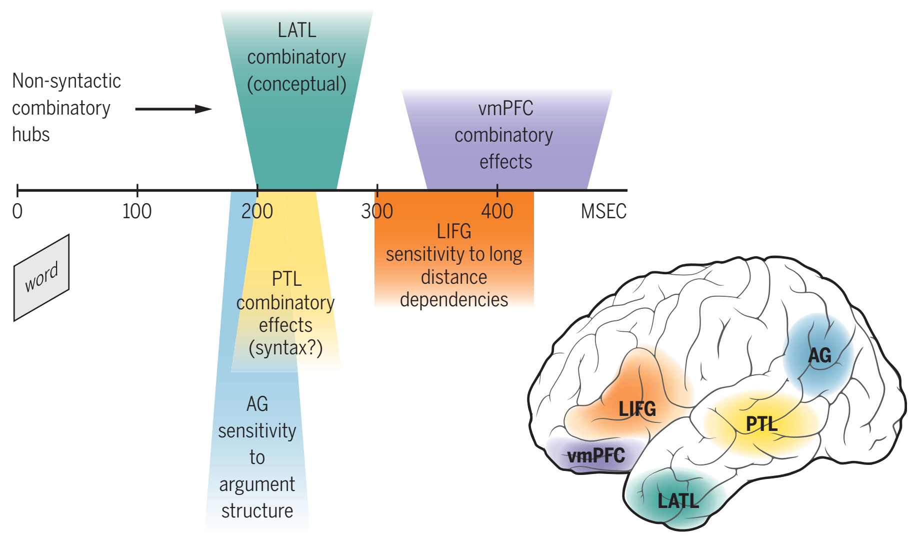

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Fig. 3. Spatiotemporal characteristics of the brain's combinatory network. The functional profiles of the activities plotted above the timeline appear nonsyntactic. The regions below the timeline represent various hypotheses for cortical loci of syntactic processing.

either syntactic or semantic, but bottom-up composition would be entirely semantic.

Another way tacit syntactic knowledge could manifest in neural signals is if we measure brains while they explicitly think about this knowledge. In fact, many neuroimaging studies use grammaticality judgments as the experimental task: Participants indicate whether the presented expression is grammatical or not (*4*, *8*). A caveat of this approach is that thinking about our syntactic knowledge may markedly differ from simply using the knowledge.

Nevertheless, it is too early to conclude that syntactic composition is not part of the brain's online combinatory machinery. Most of the necessary experiments remain to be done. For example, two-word phrases may simply be too small to drive the syntactic engine. In fact, when adjective–noun combinations were embedded in full sentences in a more intricate design, the posterior temporal cortex, associated with syntax in a recent model (*51*), showed a previously unidentified effect that reflected structure, not meaning (*19*). To test whether the syntactic engine needs some minimal amount of material before kicking into gear, studies should incrementally increase phrase size (*17*)—though even then, the challenge of distinguishing syntactic from semantic effects remains.

Outlook

Our understanding of the neurobiology of composition is progressing. From characterizations of how minimal phrases affect the brain, we gain a foundation for understanding more complex phenomena. We will also want to understand how the neurobiology of minimal composition relates to simpler processing, such as associating two elements without semantically combining them. Computational advances have improved our ability to extract knowledge from data. For example, application of multivariate pattern analysis to time-resolved electrophysiological signals allows us to inquire when, during the processing of a stimulus, a particular representation is active (*52*). This ability enables investigations into how composition affects representations of individual words (*10*). Computational modeling of language has also brought linguistic theory to the center stage of the cognitive neuroscience of sentence processing, as computational modeling benefits from the broad models of sentence structure that linguistic theory offers. Thus, an interdisciplinary synergy begins. Although we remain far from understanding how our brains create the meanings of natural language, the path forward is becoming less and less foggy.

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