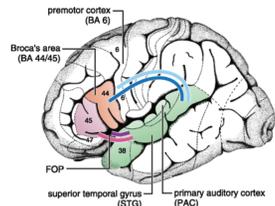


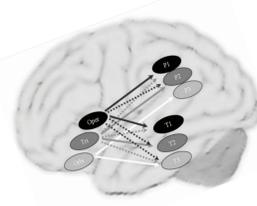
The neurobiology of grammar

Language comprehension engages functionally distinct large-scale networks in both hemispheres. Evidence indicates that they form two neurobiologically separable systems: one distributed across bilateral fronto-temporal regions, and another encompassing fronto-temporal regions in the left hemisphere (1,2).

Currently dominant models of language comprehension (3,4) link all grammatical processes to the combinatorial mechanisms supported by the left hemisphere system



Friederici et al dissociate between simple linear and complex non-linear grammatical computations, linked to LH ventral and dorsal streams respectively

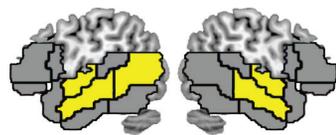


Hagoort and colleagues argue for a single mechanism of incremental sequence processing, with differences in memory requirements for simple and complex strings supported by LH BA 44/45

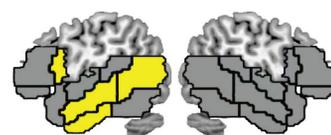
While the link between complex grammatical strings and the LH system seems unambiguous, evidence shows that simple grammatical computations can be supported bilaterally:

1. in healthy participants, the processing of syntactically simple linear utterances often engages bilateral temporal structures only
2. in patients, damage to left fronto-temporal regions does not necessarily affect the ability to understand canonical subject-verb-object sentences in English

Our recent study (Bozic et al, under review) also showed that simple grammatical computations (minimal phrases, *I play*) engage the bilateral system, while computationally demanding grammatical combinations (inflected forms, *played*) require the involvement of the LH system.



Bilateral temporal activity for minimal phrases (*I play*)



Left-lateralised fronto-temporal activity for inflected forms (*played*)

These data raise the question about the distribution of computational functions across the bihemispheric and the LH systems. What type of combinatorial mechanisms can be supported bilaterally? Are the grammatical computations that engage the LH system better characterised in terms of the type of computation or the processing demands associated with it?

Materials and Methods

Spoken grammatical strings were matched on a range of psycholinguistic variables and divided into 5 categories, varying in the type of grammatical combination and the processing demands associated with their computation.

Linear short strings (*They listen*) are minimally complex grammatical sequences, which serve as a linguistic baseline. **Linear long** and **Linear insert** strings (*I go home*; *We often run*) employ comparable left-to-right grammatical combination, but bring about an additional increase in processing and memory demands. **Non linear** strings (*Today I work / Who can I trust*) employ complex syntactic transformations such as topicalisation or wh-movement. Finally, **past tense** strings (*You agreed*) are complex, computationally demanding grammatical sequences, previously shown to engage the LH system.

Condition	Description	Example
Linear short (AB)	Linear concatenated elements	<i>They listen</i>
Linear long (ABC)	Extended string of linear concatenated elements	<i>I go home</i>
Linear insert (A#B)	Linear, with a minimal non-adjacent dependency	<i>We often run</i>
Non linear (CAB)	Non-linear, yet grammatical and complete	<i>Today I work / Who can I trust</i>
Past tense (AB+ed)	Linear concatenated elements, plus verb inflection	<i>You agreed</i>

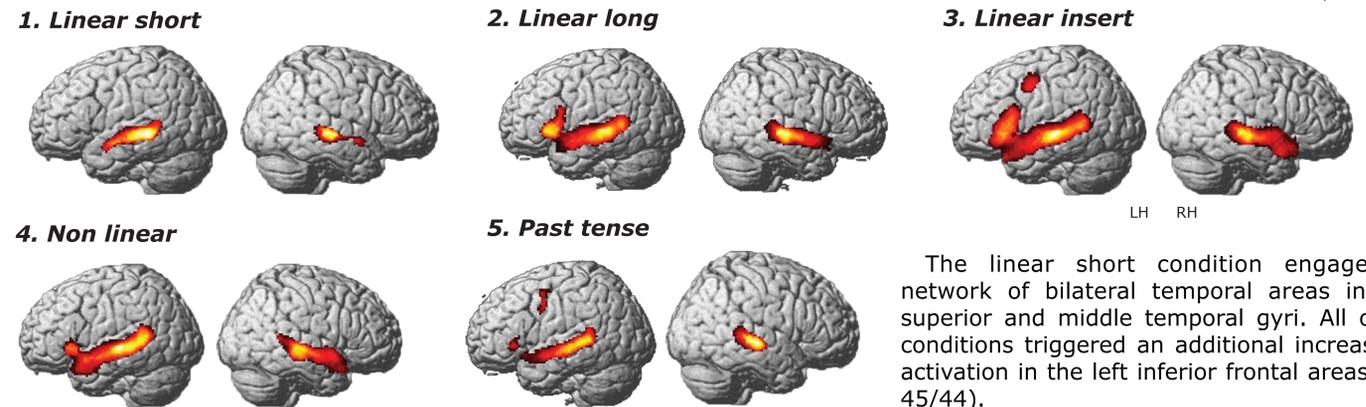
There were 40 items in each of the five conditions, for a total of 200 spoken sequences.

Spoken sequences were mixed with 200 acoustic baseline trials (musical rain, MuR), and 100 silence trials. Each grammatical sequence was presented twice. Participants listened to them passively and occasionally performed a one-back semantic task. 18 participants were scanned on a 3T Siemens system, using a fast sparse protocol (TR=3.6s, TA=2s). Data were modelled as epochs and analysed in SPM8

Condition-specific activity

Simple subtractions against the matched acoustic baseline (MuR)

p<.001 voxel, p<.05 cluster corrected for multiple comparisons

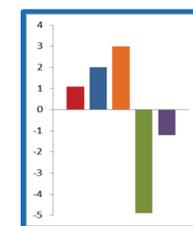


The linear short condition engaged a network of bilateral temporal areas in the superior and middle temporal gyri. All other conditions triggered an additional increase in activation in the left inferior frontal areas (BA 45/44).

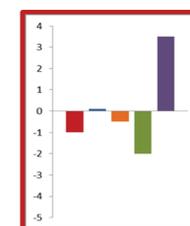
Multivariate Linear Analysis

Testing the relationship between the predictors (GLM) and the data, using the multivariate linear approach implemented in the MLM toolbox (5). Conditions are classified on the basis of the activation they trigger (relative to the MuR baseline) to calculate the orthogonal eigencomponents that minimise the within group variation and maximise the between group variation

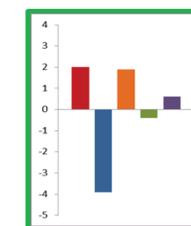
The results revealed that both the type of grammatical combination and the processing demands they elicit contribute to the condition-specific activation patterns



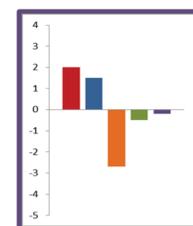
First component dissociates linear sequences from the two more complex conditions, and has a clear bilateral temporal distribution. This component accounts for 38% of the overall variance.



Second component shows that non-linear sequences and past tense sequences differ in the pattern of activity they trigger. It has a weakly left-lateralised posterior distribution, and accounts for 29% of the overall variance.

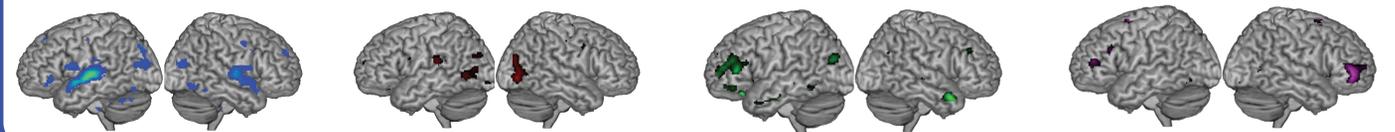


Third component distinguishes the linear long condition from the other two linear conditions, and has a left frontal distribution. This component accounts for 19% of the variance but its functional significance is unclear.



Fourth component dissociates the most processing- and memory-demanding linear insert condition from the other linear conditions, with a clear bilateral frontal distribution. This component accounts for 16% of the variance.

Bar graphs are in the unit of the beta images. Brain overlays at t > 2



Summary and Conclusions

Current models link all grammatical processes to the LH processing mechanisms, but the evidence shows that bilateral temporal regions can support simple grammatical computations.

Our data confirm that minimally complex linear grammatical strings (linear short) are supported bilaterally. All other types of grammatical combination engaged the LH inferior frontal areas BA 44/45 as well.

Multivariate linear analyses revealed that both the type of grammatical combination and the processing demands they elicit contribute to the condition-specific activation patterns.

Simple categorical distinctions provide only a poor account of the multiple mechanisms that support the processing of grammatical strings and determine the involvement of the underlying processing networks.