Distribution of grammatical functions across bihemispheric and left perisylvian networks

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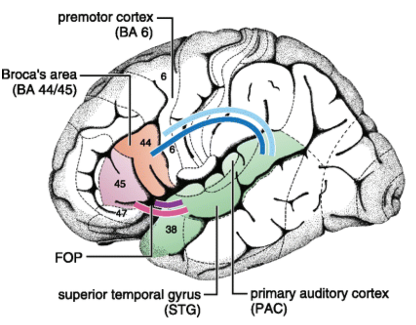
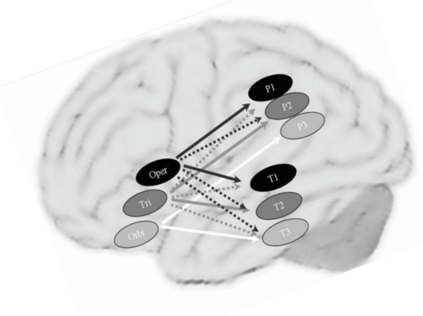
The neurobiology of grammar

Language comprehension engages functionally distinct large-scale networks in both hemispheres. Converging 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 (*Marslen-Wilson & Tyler, 2007; Bozic et al, 2010*).

Currently dominant models of language comprehension (*Hagoort 2013; Friederici 2011*) 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

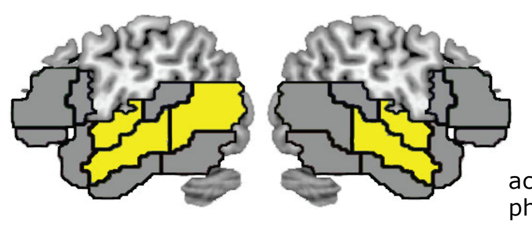


Hagoort and colleagues argue for a single mechanism of incremental sequence processing, with differences in memory requirements for simple and complex strings supported by LH BA 44/45

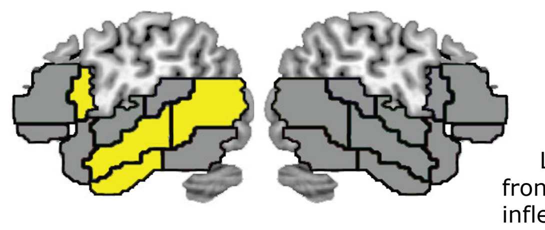
While the link between complex grammatical strings and the LH system seems unambiguous, evidence shows that simple grammatical computations can be supported bilaterally:

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, submitted*) also showed that simple grammatical computations (minimal phrases, *I play*) engage the bilateral system, while computationally demanding grammatical combinations (inflected forms, *play+ed*) 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 grammatical functions across the bihemispheric and the LH systems. What aspects of grammatical function can be supported bilaterally? What defines the grammatical computations that engage the LH system, and are they better characterised in terms of the type of combination (cf *Friederici et al*) or the processing demands associated with their computation (cf *Hagoort et al*)?

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

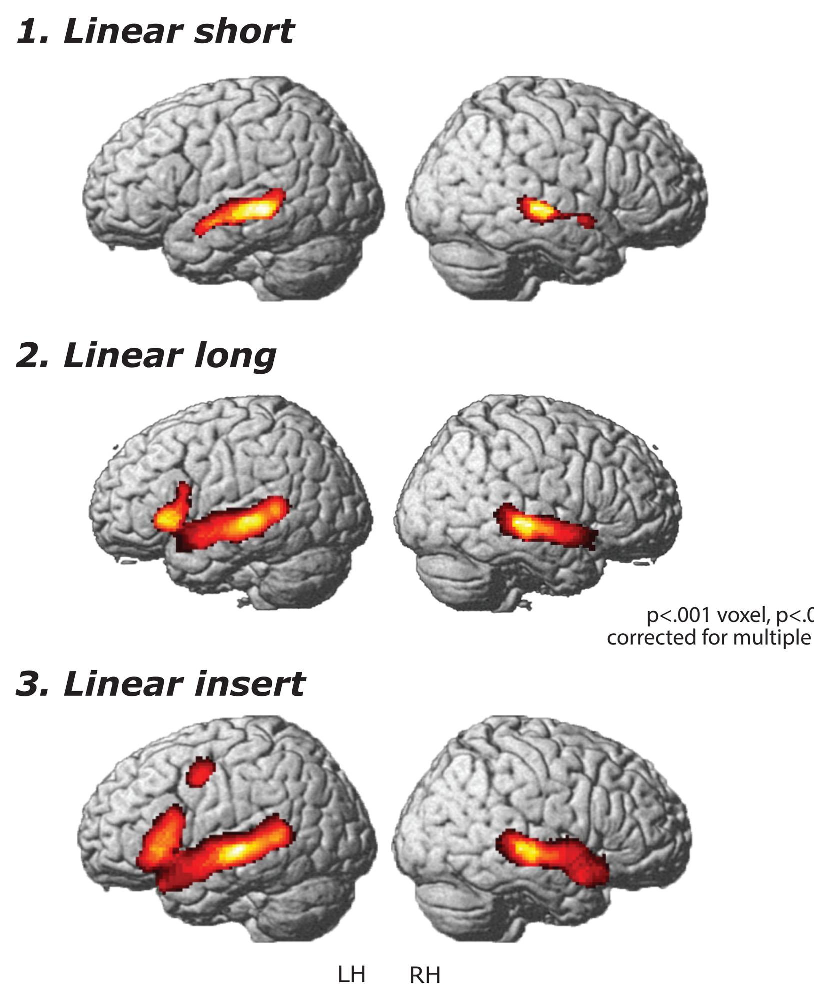
There were 40 items in each of the five conditions, for a total of 200 spoken sequences.

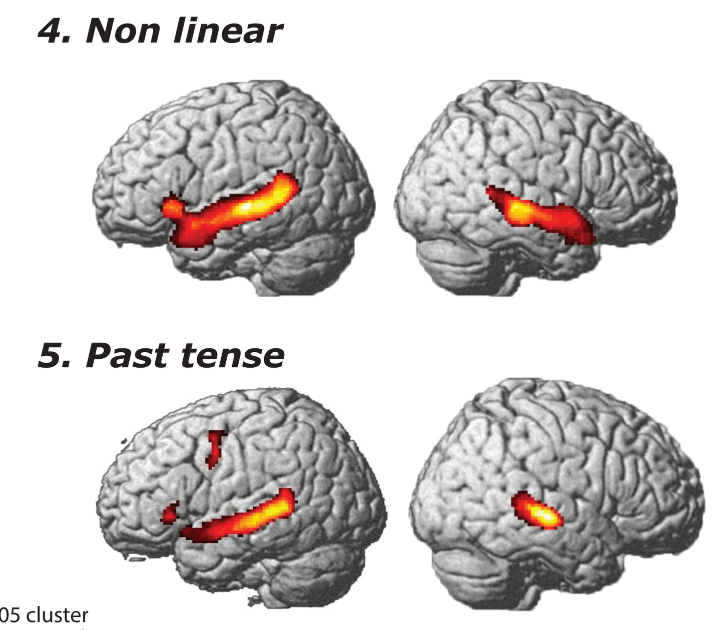
Spoken sequences were mixed with 200 acoustic baseline trials (musical rain, MuR), and 100 silence trials. Each grammatical sequence was presented twice. Participants listened to them passively and occasionally performed a one-back semantic task.

Imaging procedure: 18 participants 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, using univariate approaches and multivariate Representational Similarity Analyses *(Kriegeskorte et al, 2008)*

Condition-specific activity

Simple subtractions against the matched acoustic baseline (MuR)





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

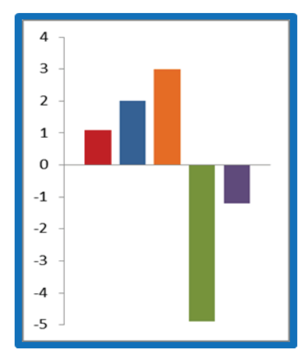
The linear short condition engaged a network of bilateral temporal areas in the superior and middle temporal gyri. All other conditions triggered an additional increase in activation in the left inferior frontal areas (BA 45/44).

Multivariate Linear Analysis

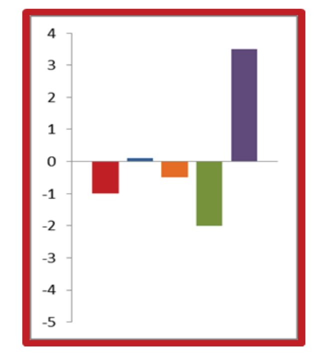
An exploratory analysis testing the relationship between the predictors (GLM) and the data, using the multivariate linear approach implemented in the MLM toolbox *(Kherif et al, 2002)*.

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

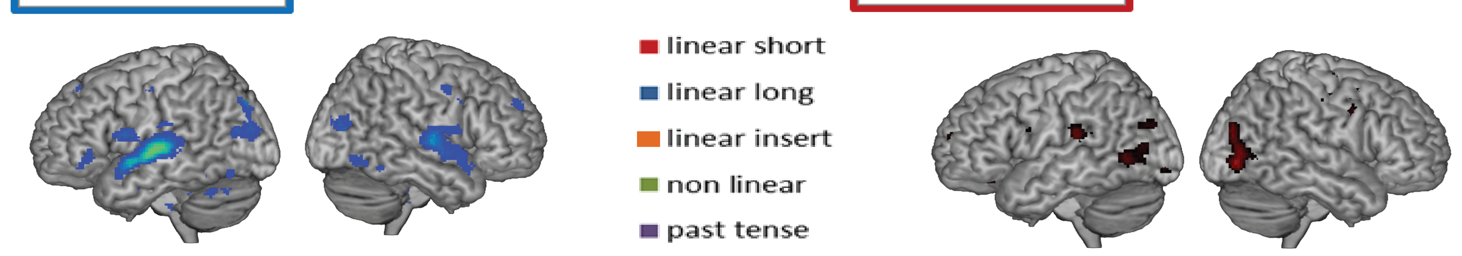
The results revealed that both the type of grammatical combination and the processing demands they elicit influence the condition-specific activation patterns

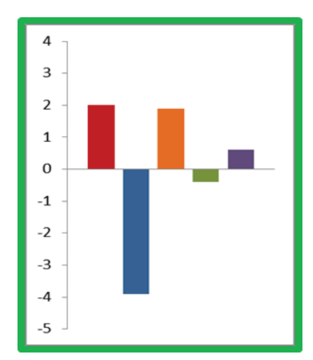


First component dissociates linear sequences from the two more complex conditions, and has a clear bilateral temporal distribution. This component accounts for 38% of the overall variance.

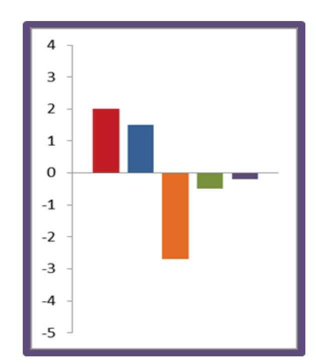


Second component shows that non-linear sequences and past tense sequences differ in the pattern of activity they trigger. It has a weakly left-lateralised posterior distribution, and accounts for 29% of the overall variance.

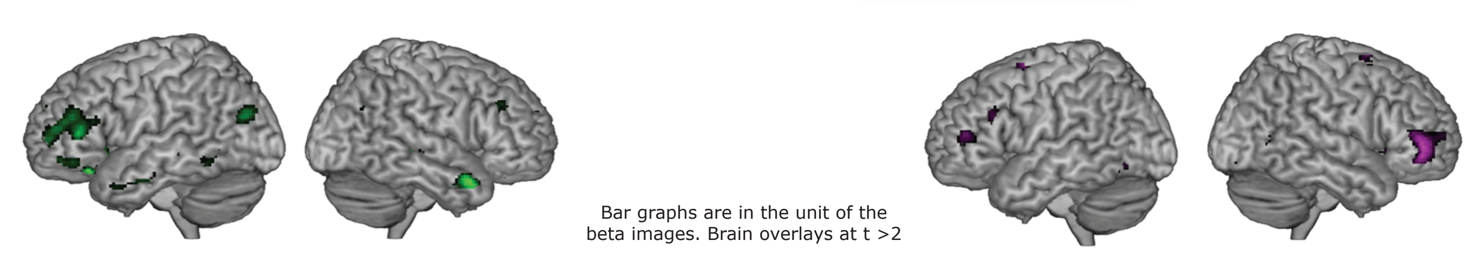




The functional significance of the third component is unclear. It distinguishes the linear long condition from the other two linear conditions, and has a left frontal distribution. This component accounts for 19% of the variance.



The 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.



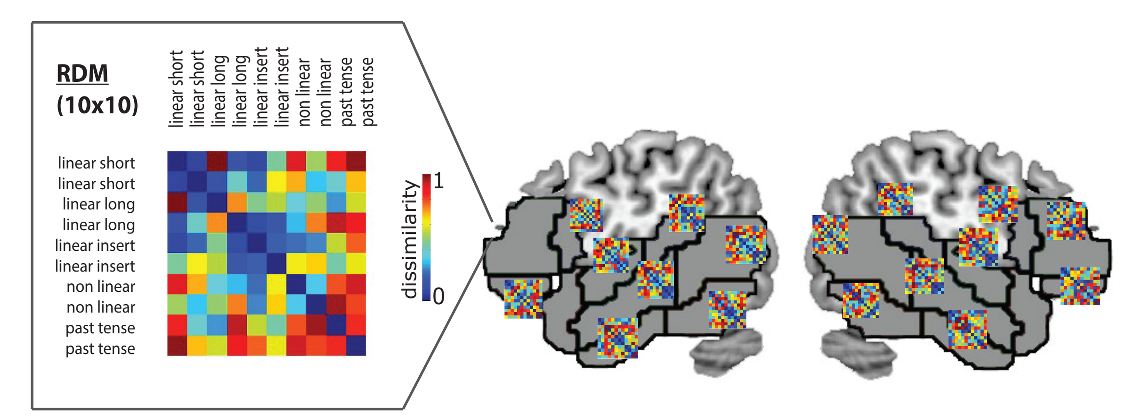
Bar graphs are in the unit of the beta images. Brain overlays at t >2

Representational Similarity Analysis

RSA is a multivariate pattern analysis method that allows us to assess the information carried by a pattern of activation across multiple voxels.

In RSA, patterns of activation are expressed as Representational Dissimilarity Matrices (RDMs), which show the correlation distance (1 - r) between activation patterns elicited by pairs of different conditions. Inference is drawn from a second level analysis that compares RDMs to theoretical models, also characterized by RDMs.

1. RDMs extracted for anatomically defined regions of interest



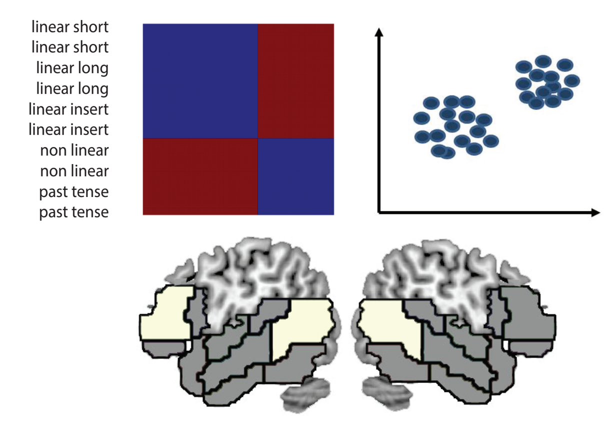
Regions of Interest (bilaterally)

Pars opercularis (BA 44)
Pars triangularis (BA 45)
Pars orbitalis (BA 47)
Superior temporal gyrus (BA 22)
Middle temporal gyrus (BA 21)
Inferior temporal gyrus (BA 20)

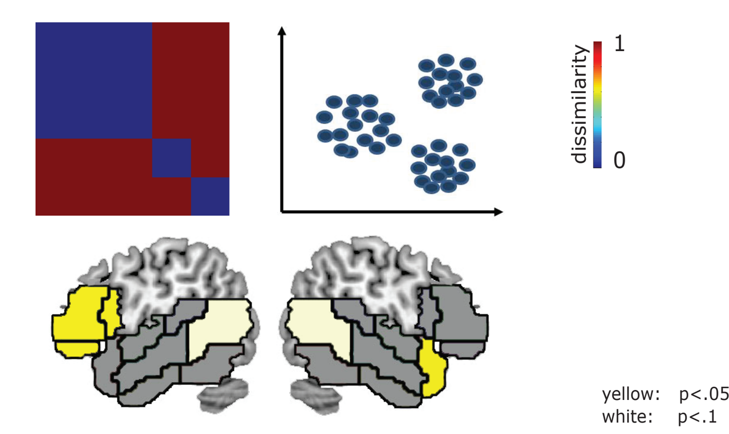
(all temporal regions further split into anterior and posterior parts)

2. RDMs compared to theoretical models

Model 1 tests for categorical distinctions in the type of grammatical combination. Specifically, this model assumes that all linear sequences create similar activation patterns, which are dissimilar to those triggered by non-linear and past tense items. Blue indicates high correlation between activation patterns, red indicates the absence of correlation. As can be predicted from the MLM results, this rudimentary model shows a very poor fit, with only marginal effects in L BA 45 and pMTG bilaterally.



Model 2 also assumes that all linear sequences trigger comparable activation patterns, dissimilar to those for non-linear and past tense sequences, but it also further differentiates between the patterns for non-linear and past tense sequences. As can be predicted from the MLM results, this more differentiated model produces a better fit, showing significant effects in left IFG and right temporal pole, in addition to marginal effects in pMTG bilaterally.



Consistent with the MLM results, RSA data confirm that simple categorical distinctions provide only a poor account of the multiple mechanisms that support the processing of grammatical strings. We need to develop more fine-grained metric in order to capture the relative contributions of the type of grammatical combination, the processing demands it elicits, and the interactions between these two dimensions.

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.

We tested what aspects of grammatical function can be supported bilaterally, and what defines the grammatical computations that engage the LH system.

Data showed 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 multiple variables - related to both the type of grammatical combination and the processing demands they elicit - determine the involvement of the underlying processing networks.

Representational Similarity Analyses confirmed that simple categorical distinctions provide only a poor account of the multiple mechanisms that support the processing of grammatical strings.

References

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