Domain-general and domain-specific computations in single word processing

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Abstract

Language comprehension relies on a multitude of domain-general and domain-specific cognitive operations. This study asks whether the domain-specific grammatical computations are obligatorily invoked whenever we process linguistic input. Using fMRI and three complementary measures of neural activity, we tested how domain-general and domain-specific demands of single word comprehension engage cortical language networks, and whether the left frontotemporal network (commonly taken to support domain-specific grammatical computations) automatically processes grammatical information present in inflectionally complex words. In a natural listening task, participants were presented with words that manipulated domain-general and domain-specific processing demands in a 2 x 2 manner. The results showed that only domain-general demands of mapping words onto their representations consistently engaged the language processing system during single word comprehension, triggering increased activity and connectivity in bilateral frontotemporal regions, as well as bilateral encoding across multivoxel activity patterns. In contrast, inflectional complexity failed to activate left frontotemporal regions in this task, implying that domain-specific grammatical processing in the left hemisphere is not automatically triggered when the processing context does not specifically require such analysis. This suggests that cortical computations invoked by language processing critically depend on the current communicative goals and demands, underlining the importance of domain-general processes in language comprehension, and arguing against the strong domain-specific view of the LH network function.

Keywords: language, fMRI, domain-general, domain-specific, connectivity, multivariate

1. Introduction

Language comprehension is a complex cognitive task that involves seamless coordination between many processes that include, but are not limited to, analysing complex perceptual information, combinatorial operations, short- and long-term memory retrieval, selecting amongst competing alternatives, processing local and hierarchically-nested dependencies and so on. While many of these processes are found across multiple cognitive functions and are considered domain-general, combinatorial grammatical operations are taken to be the core, domain-specific, foundation of the human language function. This raises the question of whether grammatical operations are obligatorily invoked whenever we process linguistic information. The current study addresses this question by investigating how domain-general and domain-specific processing demands of a well-controlled set of single words activate cortical language networks. In particular, we ask whether the domain-specific grammatical computations triggered by inflectionally complex words automatically engage the left frontotemporal network, commonly taken to represent the neural basis of language capacity.

Language comprehension engages a distributed set of regions in frontal and temporal cortices bilaterally, with their involvement varying depending on the complexity of the input and task demands (Bozic et al., 2010; 2015; Hagoort, 2014; Poeppel 2014; Marslen-Wilson & Bozic 2018). Within this distributed processing system, the left hemisphere frontotemporal network (primarily involving portions of left inferior frontal and middle and superior temporal gyri) is widely assumed to underpin grammatical computations in the key combinatorial language domains of inflectional morphology and syntax. However, the existing neurocognitive accounts provide different views on how the LH frontotemporal network supports these computations, and the extent to which this processing is unique to language. Some authors argue that this network supports a focused set of obligatory, domain-specific analyses of syntactic dependencies (Berwick et al., 2013; Santi & Grodzinsky, 2010; Zaccarella & Friederici, 2015) independently of short-term memory (Makuuchi et al., 2009) or semantic processing (Schell et al., 2017). Others attribute language-specific functions to isolated sub-regions of this network that are adjacent to those performing domain-general computations (Fedorenko, 2014; Blank & Fedorenko 2017). In this view, the domain-specific mechanisms are recruited whenever the system encounters a grammatically-structured input, while any domain-general processes in the adjoining regions will only be triggered once the input becomes sufficiently effortful. Campbell & Tyler (2018) also make a case for the domain-specificity of the left frontotemporal network, which they argue supports core syntactic operations. In contrast, other authors emphasise the role of the left inferior frontal regions in domain-general operations related to cognitive control, working memory or selection amongst competing alternatives (Novick et al., 2010, 2014; Rogalsky & Hickok, 2011), and argue that none of the left frontal activations are language-specific (Kaan & Swaab, 2002). Hagoort (2014, 2017) assigns left inferior frontal gyrus (LIFG) the role of syntactic or semantic unification (in BA44/45 and BA47 respectively), the process of on-line assembly of lexical building blocks into larger structures. These processes are supported by the executive control mechanisms in dorsolateral prefrontal cortex and anterior cingulate, in conjunction with memory storage and retrieval in the L temporal regions. In this view, LIFG operations are not language-specific, but realize a language-relevant unification function. Yet other approaches argue that LH frontotemporal activations represent the generating and updating of top-down prediction about the upcoming linguistic input, but that these operations are contextually dependant and not unique to language (Blank & Davis, 2016; Carbajal & Malmierca, 2018; Cope et al., 2017). This view is also in line with evidence that information processing within the prefrontal areas is highly dynamic and task-oriented (Haller et al., 2018; Kim et al., 2017; Yeo et al., 2015). For instance, a meta-analysis of fMRI results by Yeo et al., (2015) showed that the lateral prefrontal cortex is largely functionally flexible, with the LIFG consistently recruited for various language tasks (covert naming, word generation, semantic discrimination), but not routinely linked to passive listening of sentences – a finding that does not square well with the strong domain-specific view of LIFG function that predicts its consistent recruitment for the processing of any grammatically-structured sequence.

The functional and computational role of the wider bilateral frontotemporal network in language processing is less well explored. While the contribution of bilateral temporal areas to sound-to-meaning mapping is well established (Hickok & Poeppel, 2007; Marslen-Wilson et al., 2014), extended bilateral frontotemporal engagement has been reported primarily for contexts where comprehension becomes particularly demanding. For instance, Bozic et al. (2010; 2013) have shown that bilateral frontotemporal areas are strongly engaged by spoken words that have embedded stems (e.g. *clay* in *claim*), which trigger competition between the co-activated cohort members and the need for top-down selection between them (Marslen-Wilson 1987). Since processes of selection and control are not unique to language and are common to a range of cognitive functions, from visual perception to working memory (Miller & Cohen, 2001), this has been taken as a signature of domain-general processing in language comprehension. In addition, the RH areas engaged in language comprehension were shown to be less stable in their connectivity than LH core language areas, arguably implying their greater functional flexibility (Chai et al., 2016).

In sum, the left and the bilateral frontotemporal networks are thought to support distinct language-related functions, with prominent arguments that at least some parts of the LH network are specialised for domain-specific grammatical processing and automatically recruited by the linguistic input. However, the existing evidence is mixed, partly because the studies exploring this question tend to use heterogeneous language tasks and materials to tap into the underlying operations. These can range from single word comprehension to processing complex sentences and passages under different task requirements (e.g., passive listening, semantic or grammatical judgement, priming, memory tasks etc.), which are bound to invoke different cognitive processing demands; making it difficult to determine the extent to which the proposed language-selective frontotemporal areas instantiate obligatory computations related to grammatical properties of words, phrases or sentences.

The current study aims to overcome this issue by using a well-controlled set of single words to investigate how domain-general and domain-specific processing demands activate cortical language networks. To tap into the domain-specific grammatical processing we are using inflectional morphology, a combinatorial mechanism that binds stems and suffixes to convey grammatical information (e.g., *play+ed*), and requires grammatical analysis of the stem+suffix structure. The domain-general operations were defined as increased processing demands associated with word segmentation, as well as the competition between full forms and their onset-embedded stems. Critically however, neither of these two processes are unique to language, as both chunking the input into salient elements and competition between perceptual alternatives occur across other cognitive domains too. There were four experimental conditions that manipulated the presence of domain-general and domain-specific processing demands in a 2x2 manner; they are described in detail below.

1. 2. Using English morphology to test domain-general and domain-specific processing

To investigate how domain-general and domain-specific operations engage cortical language networks in a focused and well-controlled manner, we tested the cortical processing of English inflectionally complex words. Inflectional morphology is a key grammatical device in language, where verb or noun stems are combined with grammatical suffixes to adjust them to the grammatical requirements of the environment (e.g., changing their tense by adding *–ed, walk–walked*, or their number by adding *–s, dog-dogs*), but without changing their meaning. There is strong evidence that processing regular inflections engages left frontotemporal regions, with activation in this network observed across languages and imaging modalities (Bozic et al., 2010; Fonteneau et al., 2014; Leminen et al., 2011; Shtyrov et al., 2005; Szlachta et al., 2012), and patients with damage to these areas showing profound impairment in processing regularly inflected words (Longworth et al., 2005). This activation was most commonly taken to reflect the specifically grammatical operations associated with the combinatorial implications of the stem + suffix structure, where the relevant linguistic elements need to be combined and interpreted. However it has also been recognised that processing regular inflections triggers intensive cognitive control demands associated with the morpho-phonological segmentation of the stem + suffix combination, as well as the competition between the stem and the full form, both of which increase the demands of domain-general selection, decision and cognitive control (Bozic et al, 2010; Klimovich-Gray et al., 2017).

We exploited these dual computational demands of regular inflections by contrasting them to well-matched control stimuli that trigger primarily domain-general or domain-specific processing demands, whilst avoiding confounds such as variable working memory or task demands that can substantially alter the observed activations (Wright et al., 2011). In order to tap into the specifically grammatical processing we compared regular inflections with the processing of irregularly inflected words (*slept, broke*) which are equally grammatically complex but do not have the overt stem-suffix structure and therefore do not trigger the domain-general operations of segmentation and stem/full form competition. To tap into the specifically domain-general processing demands, we included a group of pseudoregular words (*trade, brand*), which are grammatically simple but have been shown to trigger automatic segmentation due to their resemblance to regular inflections (Post et al., 2008). This is driven by the presence of the so-called Inflectional Rhyme Pattern (IRP), a phonological pattern where the final consonant is coronal (d, t, s, z) and agrees in voice with the preceding segment, which is shared by all regular *-d* and *-s* inflections in English. The IRP signals that the ending of a complex word may be an inflectional affix and therefore should not be treated as part of the stem, triggering segmentation. Another feature of pseudoregulars that is loading on the general processing demands is the presence of an onset-embedded stem (*tray/trade, bran/brand*), which creates competition between the two forms and requires additional decision and selection processes to select the correct one (Bozic et al, 2010; 2013). The final group of stimuli were simple stem forms (e.g., *dream*), which did not include any potential grammatical or domain-general complexity and were not expected to trigger any additional domain-general or -specific processing demands.

To assess how the language networks respond to these processing demands, all stimuli were presented as single words in a natural comprehension task. Here participants were asked to simply listen attentively to each word and very occasionally perform a one-back recognition to maintain attention – a context that allows presenting both types of demands in a natural listening environment, but where grammatical analysis is not essential for task performance. More specifically, while both regular and irregular past tense items (*played, broke*) are grammatically complex and require computation and interpretation of their structure, these demands will be less prominent when they are presented as single words and not in a sentential context, where the grammatical information they carry affects the interpretation of the sentence (e.g., *I walk+ed to town*). If the LH network is engaged by grammatical complexity in this context, that would provide a strong indication for automaticity of such computations. On the other hand, single word presentation maintains the general processing demands associated with mapping words onto their representations, and resolving any competition between the co-activated lexical items. The presence of an embedded stem or IRP therefore increases the domain-general processing demands, and is expected to trigger stronger bilateral engagement in this context.

We used fMRI to look at three measures of neural activity that provide complementary information about the activations triggered by these different processing demands: (1) the classical amplitude changes of the BOLD signal in response to domain-general or domain-specific processing demands; (2) connectivity changes between the activated areas; (3) the fine-grained multivoxel activity patterns encoding domain-general and domain-specific operations in the language networks. Across the three types of measurement, evidence for shared activity triggered by regular inflections and the equally grammatically complex irregularly inflected words would point to the domain-specific grammatical computations. If the LH network and the LIFG in particular are automatically engaged by the presence of domain-specific grammatical computations, we would expect them to show increased activation and connectivity patterns for those conditions relative to the other two sets. On the other hand, shared activity of regular inflections and pseudoregular words would point to the domain-general operations of segmentation, selection and competition, which would be primarily expected to engage the bilateral network. Such pattern would suggest that the presence of grammatical complexity does not automatically engage the LH network, and that the activation of the language system is primarily driven by the current set of communicative goals and demands. Finally, the domain-general and the domain-specific processes might both be triggered automatically and supported by distinct functional networks.

2. Methods

2.1 Participants

19 native speakers of British English (11 female) were recruited. All participants were right-handed with no history of hearing or language problems. Participants were provided with detailed information regarding the purpose of the study and gave written consent. The study was approved by the Cambridge Psychology Research Ethics Committee and carried out in accordance with the relevant guidelines and regulations.

2.2 Stimuli and Procedure

The stimuli consisted of 160 single English words, split across four conditions: 40 regular inflected words (e.g. '*walked*', created by combining the stem verb with inflectional suffix *–ed*); 40 irregularly inflected words (e.g. '*spoke*') that are equally grammatically complex but do not have the overt structure; 40 pseudo-regular words (e.g. '*trade*') that are not grammatically complex but have the stem + IRP structure that mirrors regular past tense forms, and triggers comparable general processing demands; and 40 simple uninflected stems (e.g. '*dream*') that are neither grammatically complex nor have increased domain-general complexity. The stimuli generated a 2x2 design crossing grammatical and domain-general processing demands (Table 1).

- Insert Table 1 here -

Table 1: Experimental conditions

Condition	*Example*	*Domain-specific grammatical demands*	*Domain-general demands*
1. Regular past tense	*walked*	Y	Y
2. Irregular past tense	*spoke*	Y	N
3. Pseudoregular	*trade*	N	Y
4. Simple stem	*dream*	N	N

The 160 test stimuli were matched on length, number of syllables, number of phonemes and frequency across the four conditions (all p>.01), using the CELEX database and the English Lexicon Project resources (Baayen et al., 1995, Balota et al., 2007). The design also included 40 simple filler words, 160 items of acoustic baseline (Musical Rain, MuR), and 160 silent trials. The MuR acoustic baseline is a signal that closely tracks the acoustic properties of speech, while at the same time not being interpretable as speech (Uppenkamp et al., 2006). MuR stimuli were derived from the 160 test words by extracting the temporal envelopes of the auditory files and filling them with 10 ms fragments of vowel formants jittered in frequency and periodicity. MuR tokens are therefore matched to their respective words on length, root mean squared level and long-term spectrotemporal distribution of energy, allowing us to subtract MuR from test words and reveal specifically lexical activation for each condition.

The study employed a simple listening paradigm with an occasional one-back memory task. Participants were instructed to listen carefully to each item and on 6% of trials respond whether the item they were currently hearing was the same as the previous one. They indicated their responses by button press with their right hand (same-YES, different-NO). Only task-free trials were subsequently analysed. There were four blocks of 140 items each, pseudorandomized with respect to their type (condition, MuR, null, task, filler). Four dummy items at the beginning of each block allowed the signal to reach equilibrium. Each block lasted approximately 9 minutes. The experiment started with a short practice session outside the scanner, where participants were given feedback on their performance.

2.3 Acquisition

Data were acquired with a 3T Trio Siemens scanner at MRC Cognition and Brain Sciences Unit, Cambridge, using the fast-sparse gradient-echo EPI sequence to minimise the effects of the scanner noise during the presentation of auditory stimuli (TR = 3.4 s, TA= 2 s, echo time= 30 ms, flip angle = 78°, matrix size = 64 × 64, FoV = 192 × 192 mm, 32 slices, thickness 3 mm, 0.75 mm gap). T1-weighted structural scans were obtained for anatomical localisation (3-D MPRAGE sequence; TR = 2.25 s, echo time = 3.02 ms, flip angle = 9°, FoV = 256 × 240 × 192 mm, 192 slices, matrix size = 256 × 256 × 192 mm, spatial resolution 1 mm isotropic). Stimuli were presented within the 1.4 s silence period between scans, and at least 200 ms after the offset of the previous scan to avoid perceptual overlap between the stimulus and the scanner noise. The time between the offset of one stimulus and the beginning of another varied between 2.5 and 3 s. Block order was counterbalanced across participants.

2.4 Data analyses

The imagining data was pre-processed using the Automatic Analysis (AA) version 5 routine (Cusack et al., 2015). Pre-processing steps included: realignment and movement correction, EPI image coregistration, structural image segmentation, spatial normalisation to the MNI template and smoothing with a 10-mm Gaussian kernel. The first 4 dummy scans were discarded to allow for the steady-state magnetisation. No slice timing correction was used since the sparse-sampling imaging acquisition could render interpolation inaccurate (Perrachione & Ghosh, 2013). The data was high-pass filtered at 128 s to remove low-frequency noise. For the univariate and PPI analysis the smoothed data for each subject was analysed using the general linear model. Four sessions with 4 main event types (regular, irregular, pseudoregular and stem) were entered in the model, along with their corresponding MuR baseline, null events, and motion parameters to remove residual effects of subject movement. The BOLD response for each event was modelled with the canonical HRF. Contrast images from each subject were combined into a group random effects analysis and compared in a series of t-tests and a repeated measures ANOVA, implemented as a flexible factorial analysis with the four test conditions and subject-specific effects accounting for the between-subject variability. The reported results are significant at FDR $p<.05$ level corrected for multiple comparisons.

2.5 General Psycho-Physiological Interaction analysis (gPPI)

The PPI analyses assessed increases in connectivity between an a-priori defined seed region and all other voxels in the cortex for each of the four conditions separately, as well as combined following the 2 x 2 design. This analysis was conducted using the gPPI toolbox (McLaren et al., 2012).

First, a seed region was defined from the peak MNI coordinates emerging from the univariate analyses. The spherical mask (4 mm in diameter) was created around these coordinates and the BOLD activity of all voxels extracted across all blocks for each participant. Activity in these voxels was summarised by a single eigenvector derived using eigen-decomposition of the matrix containing activity of all masked voxels (the first component from a SVD decomposition) and removing HRF-related confounds (McLaren et al., 2012). This seed activity was then multiplied for each condition separately by the vectors of that condition's onset times and convolved with HRF, thus producing 4 condition-specific PPI regressors. These regressors were then entered into a 1st level GLM analyses (using the same parameters as above) together with condition-specific onsets, the seed region responses and the movement parameters. Simple subtractions were then used to contrast the connectivity profiles of the seed region(s) across conditions. Group level effects were assessed using the random effects analysis. Results are reported at p<.05 FDR cluster corrected threshold, unless otherwise stated.

2.6 Representational Similarity Analysis (RSA)

RSA assesses the similarity of fine-grained activation patterns across conditions, in order to provide qualitatively specific data about the type of information processed in a given brain area. As such, it can be more sensitive to the underlying processes than the amplitude-based univariate analyses, and it also allows testing explicit hypotheses about how the brain codes different language computations (e.g., Bozic et al, 2013; 2015; Carota et al, 2016). This analysis is done in native space to avoid the potential loss of information associated with normalising the data to a template, hence we used unsmoothed native space images that have been realigned and co-registered to the subject’s MPRAGE to construct GLMs. The analyses focused on the bilateral language processing network as identified by the literature (Bozic et al. 2010; 2015; Poeppel, 2014). To outline the network and assess the processes supported by specific areas within it, we defined a set of regions of interest (ROIs) covering bilateral temporal lobes (superior, middle and inferior temporal gyri, temporal poles and angular gyri) and inferior frontal gyri (BA 44, 45, 47). Regions were defined anatomically using WFU Pickatlas and transformed into each participant’s native space using the inverse version of the native-to-stereotaxic transformation matrix. Parameter estimates for each condition were used to create the Representational Dissimilarity Matrices (RDMs), encoding correlation distance (1–r, Pearson correlation across voxels) between activation patterns elicited by each pair of conditions. Each cell of an RDM represents the dissimilarity between activation patterns in two conditions. RDMs were then averaged across participants for each region and compared against three theoretical models, also expressed as RDMs. The three theoretical models tested were the baseline ‘Word’ model, followed by ‘General demands’ and ‘Grammatical processing’ models (see Results for details). The match between the data RDMs and model RDMs was tested by means of a second-order correlation distance test, which assesses the correlation distance between these matrices (Kriegeskorte et al., 2008). Statistical inference was assessed by a permutation test. The correlation between two RDMs is assessed against a null-hypothesis. The null hypothesis distribution of correlations was obtained by repeatedly randomizing the condition labels in one RDM and comparing it against the other. The number of permutations was set at 10000 and the cut-off threshold was 0.05 (corrected). In order to compare across models and determine what computations dominate the processing within each ROI, we performed an additional hierarchical regression analysis, where the activity pattern within a given ROI was taken as a dependant variable and RSA models as regressors. The baseline 'Word' model that we expected to account for most of the variance was entered first, followed by either the 'General demands' or 'Grammatical processing' model that we expected to produce a more localised fit. Results were corrected for multiple comparisons using FDR correction.

3. Results

3.1 Univariate subtractions and ANOVA

Subtracting the MuR acoustic baseline from the activation for all words, as well as in each condition separately, showed that all stimuli invoked similar activation in the core language system (Fig. 1 and Fig S1 in Supplementary Materials). Across the four conditions, consistent activity emerged in the bilateral superior and middle temporal gyri (STG/MTG) and the left inferior frontal gyrus (LIFG), in addition to some right inferior frontal gyrus (RIFG) activity primarily seen for the pseudoregular items. Activation coordinates for all words minus MuR, and for each condition minus MuR separately, are shown in Supplementary Materials (Table S1 & S2).

- Insert Figure 1 here -

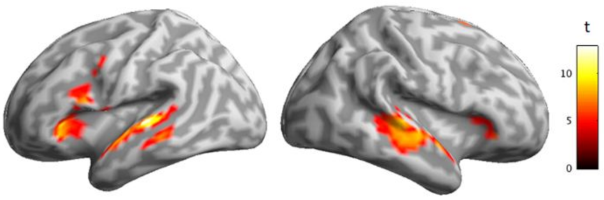
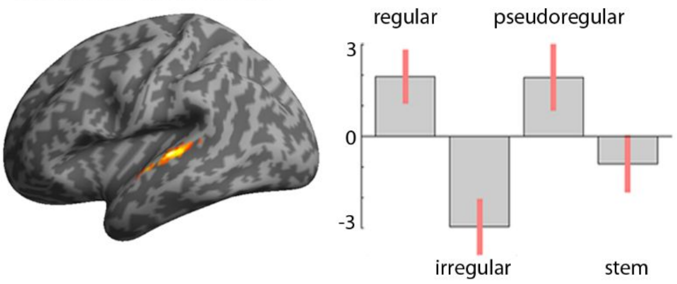


Fig. 1: Significant activation for lexical processing (all words minus MuR). FDR $p<0.05$ corrected for multiple comparisons

To identify cortical areas that were differentially activated across the four conditions we run a fixed effects ANOVA with condition and subject as main effects (see Methods for details). The only area that showed significant differences across the four conditions was the left temporal lobe (L MTG/STG; 394 voxels, peak at -66 -26 2; Figure 2a). The plot of the effect amplitude in the peak voxel in Figure 2a clearly shows increased activation for the two conditions that impose stronger domain-general processing demands (regular and pseudoregular). This was confirmed in a post-hoc t-test that directly contrasted their activation to that of the irregular and simple words ((regular + pseudoregular) – (irregular + stem), Figure 2b and Table 2b). The contrast of (regular + irregular) – (pseudoregular + stem), testing for domain-specific processing, did not reveal any significant activation. Table S3 in the Supplementary Materials shows the complementary results of all significant post-hoc comparisons between individual conditions in the left temporal cluster. The ANOVA also showed a smaller cluster in right MTG/STG (67 voxels, peak at 64 -8 -4) that had the same pattern of increased responses to the domain-general processing demands, however this cluster was below the significance threshold (Supplementary Materials, Figure S2 and Table S4). We also tested for potential differences between conditions in the LIFG by defining it as a region of interest and running both ANOVA and pairwise t-tests within this ROI. No differences between conditions emerged in any of the analyses.

- Insert Figure 2 and Table 2 here -

(a) ANOVA main effects



(b) post-hoc t-test of domain-general processing

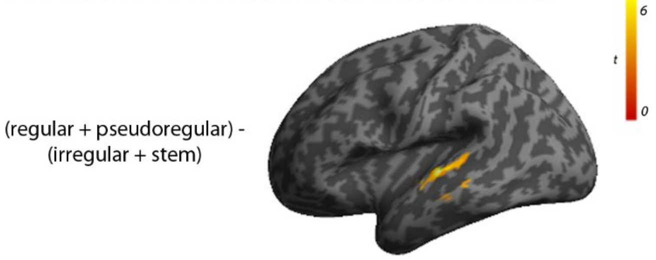


Fig.2: ANOVA results. (a) Significant differences across the four conditions, as revealed by the main effect ANOVA (FDR $p<0.05$ corrected for multiple comparisons). Right: amplitude of the effect per condition in the peak voxel, expressed in the unit of β images (b) post-hoc t-test of domain-general processing in the L temporal cluster [(regular + pseudoregular) – (irregular + stem)]

Table 2: Results of ANOVA and post-hoc tests, showing increased L temporal activity for domain-general processing

Regions	Extent	Voxel Z	Peak Coordinates		
			x	y	z

(a) ANOVA main effect					
L Middle Temporal Gyrus (BA21)	**394**	**4.82**	**-66**	**-26**	**2**
L Middle Temporal Gyrus (BA21)		4.19	-54	-28	2
L Superior Temporal Gyrus (BA22)		4.16	-64	-16	0
(b) (Regular + Pseudoregular) – (Irregular + Stem)					
L Superior Temporal Gyrus (BA22)	**272**	**4.42**	**-60**	**-18**	**2**
L **Superior** Temporal Gyrus (BA22)		3.76	-64	-14	-6
L Middle Temporal Gyrus (BA21)		3.61	-60	-32	2

Results are significant at FDR p < .05 cluster level corrected for multiple comparisons. The three most significant peaks of the cluster are shown.

This set of univariate comparisons indicates that all single words in our experiment activated the classical language system. Within this network however, the areas in the middle and superior temporal gyri (MTG/STG) showed preferential activity increases for the regular and pseudoregular conditions, which load more strongly on the domain-general demands associated with the segmentation of the stem + IRP combination, and the competition between the full form and its embedded stem (*play-played; tray-trade*). However, since any given area's operations may critically depend on the connectivity with other areas, similar BOLD amplitudes for a pair of conditions do not necessarily imply that the same computations are being carried out. We therefore next looked at the connectivity profile of the significant L temporal cluster for each condition separately using the gPPI method.

3.2 gPPI connectivity

Since the only reliable distinction between the four conditions emerged in the L MTG/STG cluster, we took its peak response voxel as the seed for the PPI analyses. Using the gPPI analysis we asked whether and how the types of words with different domain-general and domain-specific demands modulate the connectivity of this area with the rest of the language network. Figure 3a and Table S5 (Supplementary Materials) show connectivity of L MTG seed across the brain for each condition separately.

- Insert Figure 3 here -

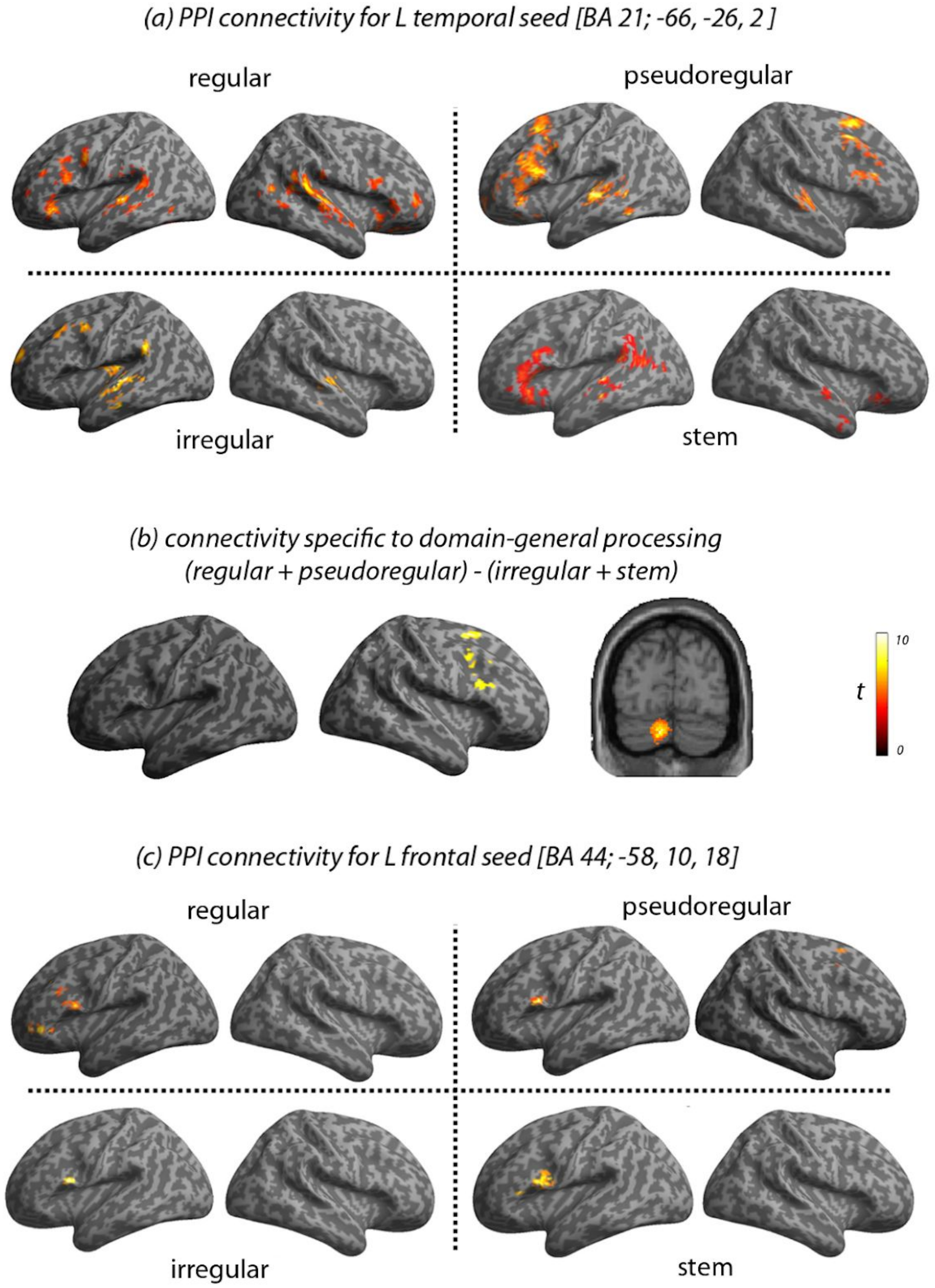


Fig 3. PPI seed connectivity results. (a) Significant connectivity for the L temporal seed for each condition separately; (b) Connectivity specific to domain-general processing, calculated by combining conditions in a 2x2 manner; (c) Significant connectivity for the L BA44 seed for each condition separately. All results significant at FDR p<0.05 cluster level corrected.

As can be clearly seen from the results, the LH temporal seed showed prominent connectivity with the frontal and temporal areas in the right hemisphere as well as L frontal regions for the conditions that are loading on the domain-general demands (regular and pseudoregular). For the remaining two conditions (irregular and stem), the results were distinctly left-lateralised, including potions of LH frontal and temporal brain regions. Unsurprisingly, a direct test of increased connectivity specific for domain-general processing ((regular + pseudoregular) – (irregular + stem)) showed effects in right frontal regions BA45 and BA8, in addition to a smaller cluster in L cerebellum (Figure 3b and Table 3). The contrast of (regular + irregular) – (pseudoregular + stem), testing for domain-specific effects, did not reveal any significant connectivity increases. Similarly, the contrast of (irregular + stem) - (regular + pseudoregular) did not show any significant connectivity increases either.

- Insert Table 3 here –

Table 3: Connectivity specific to domain-general conditions ((regular + pseudoregular) – (irregular + stem)).

Regions	Extent	Voxel Z	Peak Coordinates		
			x	y	z
R Inferior Frontal Gyrus (BA45)	**679**	**3.62**	**52**	**24**	**28**
R Middle Frontal (BA8)		3.56	24	10	60
R Middle Frontal (BA8)		3.33	28	10	52
L Cerebellum	**259**	**5.12**	**-10**	**-80**	**-32**
L Cerebellum		3.19	-18	-76	-32
L Cerebellum		2.96	-12	-80	-42

Results are significant at p<0.005 voxel and FDR p<0.05 cluster level corrected for multiple comparisons. The three most significant peaks of the clusters are shown.

Given that the previous literature linked left inferior frontal regions, and BA44 in particular, to domain-specific grammatical computations, we also tested the connectivity of this area (coordinates at -58 10 18, as obtained from the main lexical contrast shown in Fig 1 and Table S1) with the rest of the brain for each of our four conditions. Results are presented in Fig 3c. As can be seen, BA 44 showed primarily short-range L frontal connectivity for all conditions, in addition to connectivity with the neighbouring areas BA45 and BA47 for the regularly inflected words. There were no significant differences in BA44 connectivity across the four conditions, and direct tests of increased connectivity for the pairs of domain-general and the domain-specific conditions also failed to show any significant effects. This suggests that this area's connectivity supports similar computations for all test words during single word comprehension, regardless of their loadings on the domain-specific or domain-general demands.

3.3 Representational Similarity Analysis

Finally, we used RSA to assess the informational patterning of neural activity triggered by the four conditions, and to perform more specific tests of the qualitative properties of computations supported by different cortical areas. The analyses focused on the bilateral language-processing system identified in the existing literature (see Methods). Within each ROI, the activation pattern across all voxels for each condition was extracted and correlated pairwise with the activation pattern for every other condition. The results are expressed as matrices of (dis)similarity between pairs of conditions (RDMs), with each cell of an RDM representing the correlation distance (1 – r) between activation patterns elicited by a pair of conditions. Each RDM was then compared against models (also expressed as RDMs) that represent specific hypotheses about the underlying processing computations. Results are presented in Figure 4 below, and Tables S6 and S7 in the Supplement.

- Insert Figure 4 here –

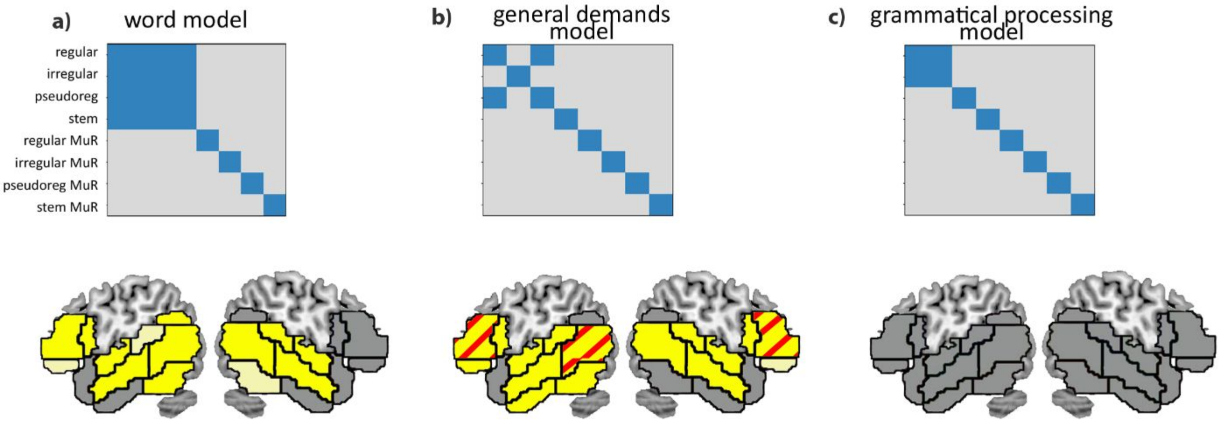


Fig. 4: RSA results. Top panel: model RDMs (a) Word, (b) General Demands and (c) Grammatical Processing model. Blue indicates correlated activation patterns due to a shared property, grey – absence of correlation; Bottom: ROIs displaying significant model fit for each of the models are marked in yellow. ROIs marked with red stripes in the General Demands model show residual significant model fit after removing effects of the Word model and FDR correction for the *n* of ROIs tested.

The 'Word' model tested which regions show sensitivity to lexical processing, regardless of the computational requirements of the words involved. This model assumes that any lexical item creates an activation pattern that is similar to the pattern triggered by other lexical items, but which is dissimilar to the pattern triggered by the acoustically-matched MuR baseline. As described in Methods, this model was expected to account for most of the variance in the language network, and was used as a reference point for assessing the fit of the subsequent models of domain-general and domain-specific operations. Predictably, and consistently with the univariate subtraction of all words minus MuR (Figure 1), this model produced a significant fit in bilateral temporal and left frontal areas that are critical for lexical recognition and analysis (average r=0.43).

The other two models grouped conditions based on their domain-general and domain-specific processing demands. The 'General demands' model groups together regularly inflected words with pseudoregulars, assuming that these stem + IRP combinations trigger similar activation patterns, and asking where in the language system can we detect increased sensitivity for the processing demands associated with morpho-phonological segmentation and competition between simultaneously activated forms. The results showed a significant fit in a large bilateral frontotemporal network (r=0.30), consistent with the existing evidence on the involvement of this network in the domain-general aspects of language processing (Bozic et al, 2010; 2013; Marslen-Wilson et al, 2014). Testing for regions where this process statistically dominates over and above the general lexical processing (the 'Word' model) revealed three regions: bilateral BA45 and left posterior MTG (Figure 4b). Finally, we tested the 'Grammatical processing' model, which groups together regular and irregular inflections that are equally grammatically complex, asking where in the network this specifically grammatical processing dominates during single word comprehension. No regions showed significant fit with this model (r=0.05) (Figure 4c).

4. Discussion

This study aimed to determine how domain-general and domain-specific demands of word processing engage the language processing networks, in terms of both their activity and connectivity patterns. In particular, we wanted to assess whether the LH frontotemporal network, commonly taken to be the domain-specific backbone of our linguistic capacity, is indeed engaged whenever the system encounters a grammatically-structured input. To do so we used a closely matched set of single words that allowed us to manipulate the presence of grammatical and domain-general complexity, while controlling for working memory and task demands. We defined domain-specific grammatical processes as those related to the grammatical analysis of past tense forms, present in regularly and irregularly inflected words (*played, spoke*). In contrast, domain-general processes were defined as those related to word segmentation and the competition between the embedded stem and the full form (*play-played; tray-trade*), both of which impose increased cognitive control demands. All stimuli were presented as single words in a natural comprehension task, which simply requires that the input is mapped onto the correct lexical representation. While the domain-general operations of segmentation and competition are intrinsic to this process and are expected here, grammatical analysis is not contextually required and its presence would therefore be a strong indication for automaticity of domain-specific computations.

Our first finding was that all conditions activated the language processing network similarly in this task. Subtracting the well-matched condition-specific MuR baseline from all words, as well as each condition separately, revealed activation in the bilateral temporal and LH frontal areas, consistent with the evidence that these areas play a key role in language processing (Tyler and Marslen-Wilson, 2007, Hagoort, 2017; Hickok & Poeppel, 2007). There were no differences in the amount of activation of the LIFG or its subparts across the four conditions, providing no evidence for differential activation of this key part of the LH network by the presence of grammatical complexity during single word comprehension. A consistent result emerged from the PPI analysis, which also showed no significant differences in left BA44 connectivity across the four conditions.

Our second and critical finding was that only stimuli with increased domain-general computational demands consistently modulated the response of the language network in this task. The ANOVA results showed activity increases in response to regular and pseudoregular forms - which share the increased domain-general demands - in left middle and superior temporal regions, with a comparable but weaker result emerging in the right temporal cortex too. In contrast, the domain-specific demands of grammatical analysis, which group regular and irregular past tense forms, were not associated with any activity increases. The subsequent PPI connectivity analysis provided complementary evidence, showing robust bilateral frontotemporal connectivity for regulars and pseudoregulars, and weaker and much more left-lateralized frontotemporal connectivity patterns for irregular inflections and stems. A direct comparison between the connectivity specifically triggered by the domain-general conditions over that of the other two sets showed increased engagement of right frontal areas (BA45/BA8) as well as the left cerebellum. This pattern of results was further confirmed by the RSA, which has shown specific responses to the presence of domain-general complexity in regulars and pseudoregulars within the bilateral BA45 and L posterior MTG, while no areas within the language processing system responded to the presence of grammatical complexity per se. Using the RSA method has been particularly important since, unlike other techniques, RSA maps cortical activity patterns within individual subjects, thus generally avoiding the issue of spatial smoothing on the group level, which has been argued to obscure the anatomically precise group-level effects in the areas with high inter-subject variability such as the IFG (e.g., Fedorenko et al., 2013). In summary, the results are consistent across all three types of measurements in showing that the demands of simple word comprehension primarily engage the domain-general computations in the bilateral frontotemporal system and do not differentially activate the LH network, even for words that are grammatically complex.

The findings about increased bilateral frontotemporal activity in response to domain-general processing demands are consistent with the existing evidence from different languages (English, Polish, Italian) that this network supports core comprehension processes of mapping spoken words onto their representations, and is particularly engaged when this process becomes demanding (e.g., due to the presence of an embedded stem and competition between it and the full form, demands of morpho-phonological segmentation or top-down selection etc; Bozic et al, 2010; 2013; Carota et al, 2016). Engagement of the extended bilateral frontotemporal network in response to domain-general demands in language processing is also in line with the literature that associates parts of this network with the multiple demand system for cognitive control (Crittenden & Duncan, 2014), auditory attentional control (Noyce et al., 2017), inhibition and response monitoring (Henson et al., 1999). The link to domain-general processes is further reinforced by the observed cerebellum activation, which has been associated with executive functions needed for language processing (e.g., Bellebaum & Daum, 2007).

In contrast to this clear recruitment of the domain-general operations during simple word comprehension, our data showed equally consistent absence of responses specific to the word's grammatical complexity across the three types of measurement. As noted earlier, the single word presentation context in which the participants were simply required to listen and understand the words does not necessarily require the analysis and interpretation of the word's grammatical structure in the same way as this would have been required if they were presented in a sentential context. This is because the role of past tense inflection (and inflectional morphology in general) is to adjust the stem to the grammatical environment in which it occurs (Bickel & Nichols, 2007), such that the information it carries determines the interpretation of the sentence (e.g., *I walk to town* vs *I walked to town*) – a role that is not utilised when words are presented outside the sentential context. As reviewed in the Introduction, the LH frontotemporal network, and the LIFG in particular, have been argued to support core grammatical operations independently of the wider processing demands that the linguistic input might be imposing onto the processing system (Makuuchi et al, 2009; Schell et al, 2017; Fedorenko, 2014). This view implies that these domain-specific language operations would need to be engaged whenever we perceive and process language at the appropriate level of complexity, taking precedence over any domain-general mechanisms that are only triggered once the input becomes sufficiently effortful. Our results suggest that this is assumption is not necessarily correct. Instead, they show that the current communicative goals and their demands, as determined by the context, appear to be critically driving the engagement of the language networks and the depth of grammatical analysis required. While this position is not necessarily incompatible with the view that the LH network supports domain-specific language operations, it implies that these operations are not automatically triggered whenever the input is sufficiently complex. Thus, our findings that domain-general operations can attain primacy when this is context-appropriate are more easily accommodated within the accounts that argue for functionally flexible and task-oriented engagement of the frontotemporal networks (Yeo et al., 2015 Furlan et al., 2018), and against the strong domain-specific view of the LH network function. They are also in line with the “good enough” view of linguistic processing (Ferreira & Patson 2007; Karimi & Ferreira, 2016), which argues that the fully-fledged grammatical analysis of utterances only becomes engaged when this is contextually required or driven by experimental instructions. It is however also necessary to note that current data only allow us to make this inference at the level of single word comprehension, which is a necessary but specific aspect of the overall language comprehension process; further research is needed to clarify how these word-level processes interact with top-down contextual constraints during sentence comprehension. In addition, the observed pattern of results might not be expected to replicate identically in non-concatenative languages like Arabic or Hebrew, where grammatical information is interleaved with semantic roots, and is therefore more likely to be automatically extracted and processed during word comprehension.

5. Conclusions

Our findings show that single word comprehension automatically triggers analysis of the domain-general characteristics related to their surface complexity. These processes engage bilateral frontotemporal areas both in terms of their activity and connectivity patterns. We found no evidence for word-related grammatical analysis, suggesting that such processes are not automatically engaged whenever grammatical information is present. These data imply that the cortical language system selectively engages only in the context-relevant aspects of the linguistic analysis.

Acknowledgements

This work was supported by the University of Cambridge RCS award to MB, and the Marie Skłodowska-Curie award (grant agreement No 798971) to AKG.

References

Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). The CELEX lexical database (release 2). *Distributed by the Linguistic Data Consortium, University of Pennsylvania*.

Balota, D.A., Yap, M.J., Cortese, M.J., Hutchison, K.A., Kessler, B., Loftis, B., Neely, J.H., Nelson, D.L., Simpson, G.B., & Treiman, R. (2007). The English Lexicon Project. *Behavior Research Methods*, 39, 445-459.

Berwick, R. C., Friederici, A. D., Chomsky, N., & Bolhuis, J. J. (2013). Evolution, brain, and the nature of language. *Trends in Cognitive Sciences*, 17(2), 89–98. http://doi.org/10.1016/j.tics.2012.12.002

Bickel, B., & Nichols, J. (2007). Inflectional morphology. *Language typology and syntactic description*, *3*(2), 169-240.

Blank, H., & Davis, M. H. (2016). Prediction Errors but Not Sharpened Signals Simulate Multivoxel fMRI Patterns during Speech Perception. *PLoS Biology,* 14(11), e1002577. http://doi.org/10.1371/journal.pbio.1002577

Blank, I. A., & Fedorenko, E. (2017). Domain-general brain regions do not track linguistic input as closely as language-selective regions. *Journal of Neuroscience*, *37*(41), 9999-10011.

Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences of the United States of America*, 107(40), 17439–44. http://doi.org/10.1073/pnas.1000531107

Bozic M, Tyler LK, Su L, Wingfield C, Marslen-Wilson WD (2013). Neurobiological systems for lexical representation and analysis in English. *Journal of Cognitive Neuroscience*. 25:1678-91.

Bozic, M., Fonteneau, E., Su, L., & Marslen-Wilson, W. D. (2015). Grammatical analysis as a distributed neurobiological function. *Human Brain Mapping,* 36(3), 1190–1201. http://doi.org/10.1002/hbm.22696

Campbell, K. L., & Tyler, L. K. (2018). Language-related domain-specific and domain-general systems in the human brain. *Current opinion in behavioral sciences*, *21*, 132-137.

Carbajal, G. V., & Malmierca, M. S. (2018). The Neuronal Basis of Predictive Coding Along the Auditory Pathway: From the Subcortical Roots to Cortical Deviance Detection. *Trends in Hearing,* 22, 1–33. http://doi.org/10.1177/2331216518784822

Carota, F., Bozic, M., & Marslen-Wilson, W. (2016). Decompositional Representation of Morphological Complexity: Multivariate fMRI Evidence from Italian. *Journal of Cognitive Neuroscience,* 28(12), 194–198. http://doi.org/10.1162/jocn

Chai, L. R., Mattar, M. G., Blank, I. A., Fedorenko, E., & Bassett, D. S. (2016). Functional Network Dynamics of the Language System. *Cerebral Cortex,* 26(11), 4148–4159. http://doi.org/10.1093/cercor/bhw238

Cope, T. E., Sohoglu, E., Sedley, W., Patterson, K., Jones, P. S., Wiggins, J., ... Rowe, J. B. (2017). Evidence for causal top-down frontal contributions to predictive processes in speech perception. *Nature Communications,* 8(1), 1-16. http://doi.org/10.1038/s41467-017-01958-7

Crittenden, B. M., & Duncan, J. (2014). Task difficulty manipulation reveals multiple demand activity but no frontal lobe hierarchy. *Cerebral Cortex*, 24(2), 532-540. http://doi.org/10.1093/cercor/bhs333

Cusack, R., Vicente-Grabovetsky, A., Mitchell, D. J., Wild, C. J., Auer, T., Linke, A. C., & Peelle, J. E. (2015). Automatic analysis (aa): efficient neuroimaging workflows and parallel processing using Matlab and XML. *Frontiers in Neuroinformatics,* 8(90), 1-19. http://doi.org/10.3389/fninf.2014.00090

Fedorenko, E. (2014). The role of domain-general cognitive control in language comprehension. *Frontiers in psychology*, *5*, 335.

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America,* 110(41), 16616–21. http://doi.org/10.1073/pnas.1315235110

Ferreira, F., & Patson, N. D. (2007). The 'good enough'approach to language comprehension. *Language and Linguistics Compass*, *1*(1-2), 71-83.

Fonteneau, E., Bozic, M., & Marslen-Wilson, W. D. (2014). Brain network connectivity during language comprehension: interacting linguistic and perceptual subsystems. *Cerebral Cortex*, *25*(10), 3962-3976.

Furlan, M., Babcock, L., & Vallesi, A. (2018). Decoding rule search domain in the left inferior frontal gyrus. *PloS one*, *13*(3), e0194054.

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Current Opinion in Neurobiology,* 28, 136–141. http://doi.org/10.1016/j.conb.2014.07.013

Hagoort, P. (2017). The core and beyond in the language-ready brain. *Neuroscience and Biobehavioral Reviews*, 81, 194–204. http://doi.org/10.1016/j.neubiorev.2017.01.048

Haller, M., Case, J., Crone, N. E., Chang, E. F., King-Stephens, D., Laxer, K. D., Weber, P., Parvazi, J., Knight, R., Shestyuk, A. Y. (2018). Persistent neuronal activity in human prefrontal cortex links perception and action. *Nature Human Behaviour,* 2(1), 80–91. http://doi.org/10.1038/s41562-017-0267-2

Henson, R. N. A., Shallice, T., Dolan, R. J. (1999). Right prefrontal cortex and episodic memory retrieval: A functional MRI test of the monitoring hypothesis. *Brain,* 122(7), 1367-1381. https://doi.org/10.1093/brain/122.7.1367

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature reviews neuroscience*, *8*(5), 393.

Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences,* 6(8), 350–356. http://doi.org/10.1016/S1364-6613(02)01947-2

Karimi, H., & Ferreira, F. (2016). Good-enough linguistic representations and online cognitive equilibrium in language processing. *The Quarterly Journal of Experimental Psychology*, *69*(5), 1013-1040.

Kim, Y.-J., Tsai, J. J., Ojemann, J., & Verghese, P. (2017). Attention to Multiple Objects Facilitates Their Integration in Prefrontal and Parietal Cortex. *The Journal of Neuroscience,* 37(19), 4942–4953. http://doi.org/10.1523/JNEUROSCI.2370-16.2017

Klimovich-Gray, A., Bozic, M., & Marslen-Wilson, W. D. (2017). Domain-specific and domain-general processing in left perisylvian cortex: Evidence from Russian. *Journal of Cognitive Neuroscience,* 29(2), 382-397. http://doi.org/10.1162/jocn_a_01047

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience,* 2(4), 1-28. http://doi.org/10.3389/neuro.06.004.2008

Leminen, A., Leminen, M., Lehtonen, M., Nevalainen, P., Ylinen, S., Kimppa, L., Sannemann C., Makela J. P. & Kujala, T. (2011). Spatiotemporal dynamics of the processing of spoken inflected and derived words: a combined EEG and MEG study. *Frontiers in human neuroscience*, *5*, 66.

Longworth, C. E., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (2005). Getting to the meaning of the regular past tense: Evidence from neuropsychology. *Journal of Cognitive Neuroscience,* 17(7), 1087–1097. http://doi.org/10.1162/0898929054475109

Makuuchi, M., Bahlmann, J., Anwander, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences of the United States of America,* 106(20), 8362–7. http://doi.org/10.1073/pnas.0810928106

Marslen-Wilson, W. D. (1987). Functional parallelism in spoken word-recognition. *Cognition*, *25*(1-2), 71-102.

Marslen-Wilson, W.D., & Bozic, M. (2018). Dual neurobiological systems underlying language evolution: inferring the ancestral state. *Current Opinion in Behavioral Sciences,* 21, 176–181. http://doi.org/10.1016/j.cobeha.2018.05.004

Marslen-Wilson WD, Bozic M, Tyler LK (2014). *Morphological systems in their neurobiological contexts*. In: Gazzaniga M (ed). The Cognitive Neurosciences. 5th edition. MIT Press.

McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *NeuroImage,* 61(4), 1277–1286. http://doi.org/10.1016/j.neuroimage.2012.03.068

Miller, E., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neroscience,* 24(1),167-202. http://doi.org/10.1146/annurev.phyto.41.052002.095656

Noyce, A. L., Cestero, N., Michalka, S. W., Shinn-Cunningham, B. G., & Somers, D. C. (2017). Sensory-biased and multiple-demand processing in human lateral frontal cortex. *The Journal of Neuroscience,* 37(36), 8755-8766. http://doi.org/10.1523/JNEUROSCI.0660-17.2017

Novick JM, Trueswell JC, Thompson-Schill SL. (2010). Broca's area and language processing: Evidence for the cognitive control connection. *Language and Linguistic Compass*, 4:906–924.

Novick JM, Hussey EK, Teubner-Rhodes S, Harbison JI, Bunting M (2014). Clearing the garden path: Improving sentence processing through executive control training. *Language Cognition and Neuroscience*, 29:186–217.

Perrachione, T. K., & Ghosh, S. S. (2013). Optimized design and analysis of sparse-sampling fMRI experiments. *Frontiers in Neuroscience,* 7(55), 1–18. http://doi.org/10.3389/fnins.2013.00055

Poeppel, D. (2014). The neuroanatomic and neurophysiological infrastructure for speech and language. *Current Opinion in Neurobiology,* 28, 142–149.http://doi.org/10.1016/j.conb.2014.07.005

Post, B., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (2008). The processing of English regular inflections: Phonological cues to morphological structure. *Cognition*, 109(1), 1–17. http://doi.org/10.1016/j.cognition.2008.06.011

Rogalsky, C., & Hickok, G. (2011). The role of Broca's area in sentence comprehension. *Journal of Cognitive Neuroscience,* 23(7), 1664-1680. http://doi.org/10.1162/jocn.2010.21530

Santi, A., & Grodzinsky, Y. (2010). fMRI adaptation dissociates syntactic complexity dimensions. *NeuroImage*, 51(4), 1285–93. http://doi.org/10.1016/j.neuroimage.2010.03.034

Schell, M., Zaccarella, E., & Friederici, A. D. (2017). Differential cortical contribution of syntax and semantics: An fMRI study on two-word phrasal processing. *Cortex*, 96, 105-120. http://doi.org/10.1016/j.cortex.2017.09.002

Shtyrov Y, Pihko E, Pulvermuller F (2005). Determinants of dominance: is language laterality explained by physical or linguistic features of speech? *NeuroImage*; 27:37–47.

Szlachta, Z., Bozic, M., Jelowicka, A., & Marslen-Wilson, W. D. (2012). Neurocognitive dimensions of lexical complexity in Polish. *Brain and Language,* 121(3), 219–25. http://doi.org/10.1016/j.bandl.2012.02.007

Tyler, L. K., & Marslen-Wilson, W. (2007). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1493), 1037-1054.

Uppenkamp, S., Johnstrude, I. S., Norris, D., Marslen-Wilson, W., Patterson, R. D. (2006). Locating the initial stages of speech–sound processing in human temporal cortex. *NeuroImage*, 31(3), 1284-1296. http://doi.org/10.1016/j.neuroimage.2006.01.004

Wright, P., Randall, B., Marslen-Wilson, W. D., & Tyler, L. K. (2011). Dissociating linguistic and task-related activity in the left inferior frontal gyrus. *Journal of Cognitive Neuroscience*, *23*(2), 404-413.

Yeo, B. T., Krienen, F. M., Eickhoff, S. B., Yaakub, S. N., Fox, P. T., Buckner, R. L., Asplund C., Chee, M. W. L. (2015). Functional specialization and flexibility in human association cortex. *Cerebral Cortex,* 25(10), 3654–3672. http://doi.org/10.1093/cercor/bhu217

Zaccarella, E., & Friederici, A. D. (2015). Merge in the human brain: A sub-region based functional investigation in the left pars opercularis. *Frontiers in Psychology,* 6(1818), 1–9. http://doi.org/10.3389/fpsyg.2015.01818