Imaging Neuroscience
an open access journal

Research Article

Syntactic processing engages the semantic control network

Qianwen Chang[a], Elizabeth Jefferies[b,*], Rebecca L. Jackson[b,*]

[a]State Key Laboratory of Cognitive Neuroscience and Learning & IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, China
[b]Department of Psychology, University of York, Heslington, Yorkshire, United Kingdom

*These authors contributed equally

Corresponding Author: Rebecca L. Jackson (rebecca.jackson@york.ac.uk)

ABSTRACT

The relationship between semantics and syntax is highly contested. Neuroimaging evidence has offered conflicting views on whether these domains are neurally separable, in part because prior work has not distinguished two key components of semantic cognition: *semantic representation* and *semantic control*. In this study, we conducted an activation likelihood estimation (ALE) meta-analysis to identify regions consistently engaged by more versus less demanding syntactic processing, and compared these directly with regions recruited by more versus less demanding semantic processing. Demanding syntactic processing engaged regions across the semantic control network (SCN), including the inferior frontal gyrus (IFG) and insula (particularly on the left), left posterior temporal cortex (posterior superior temporal sulcus and middle temporal gyrus), and bilateral dorsomedial prefrontal cortex. No regions outside the SCN responded significantly more to syntactic demands than semantic control. Within the SCN, there was significantly less reliable activation for syntactic than for semantic control demands in some anterior (pars triangularis) and ventral (pars orbitalis) portions of the left IFG and a region in posterior fusiform and inferior temporal gyrus. Greater involvement for syntax than semantic control was identified in a small region of posterior left IFG (pars opercularis) within the SCN. Moreover, both controlled semantic and syntactic processing showed multimodal responses to auditory and visual stimuli in the left IFG and posterior temporal cortex (PTC). Together, these findings suggest that syntactic processing is distinct from semantic representation, yet demanding syntax engages portions of the SCN, reflecting a shared need to access and manipulate stored semantic knowledge for flexible, context-sensitive use.

Keywords: semantic control, syntactic processing, ALE meta-analysis, multiple-demand network

1. INTRODUCTION

The relationship between syntax and semantics has long been debated. Syntactic processing involves analysing the relationship between words, including sentential structure (Friederici & Kotz, 2003), while semantic cognition allows comprehension of their meaning. Both semantics and syntax rely on statistical learning (Saffran, 2020; Thompson & Newport, 2007), and can be learnt simultaneously (Poletiek et al., 2021). Despite this, the relationship between these processes remains controversial. It is argued that syntax and semantics are orthogonal (Chomsky, 1957), that is, it is possible to manipulate either the syntactic structure or the meaning of a sentence independently without affecting the other. For example, *The dog [the cat chases] runs* and *The cat [the dog chases] runs* have identical syntactic structure but different meanings (Poletiek et al., 2021). Indeed, semantic dementia patients show a loss of semantic concepts

Received: 4 November 2025 Revision: 23 April 2026 Accepted: 29 May 2026 Available Online: 3 June 2026

The MIT Press
© 2026 The Authors. Published under a Creative Commons Attribution 4.0 International (CC BY 4.0) license.

with preserved syntactic abilities (Landin-Romero et al., 2016; Rochon et al., 2004). In contrast, agrammatic stroke and PPA patients show impaired syntactic abilities, while single-word and object comprehension are relatively spared (Bonner et al., 2010). In addition, although syntactic and semantic deficits can co-occur in aphasia patients, there is evidence for a partial dissociation between them (Casilio et al., 2019). Together, these findings have provided strong evidence that syntax and semantics are dissociable. In addition, syntax appears language specific, while the semantic network responds similarly to both verbal and nonverbal stimuli, including pictures and actions (Canini et al., 2016; Krieger-Redwood et al., 2015; Schnur et al., 2009; Sitnikova et al., 2014) and damage results in multimodal semantic deficits (Corbett et al., 2009; Jefferies & Lambon Ralph, 2006). However, simply learning to predict the next word in a sentence provides large language models with remarkable semantic and syntactic abilities, without the need to rely on distinct processes or regions (Arana et al., 2024; Contreras Kallens et al., 2023). Due to the compelling evidence on both sides of this debate, the relationship between semantic and syntactic processing remains unclear (Friederici & Weissenborn, 2007; Kako & Wagner, 2001; Pylkkänen, 2019).

Recent research may transform this debate by highlighting the multifactorial nature of semantic cognition. Semantic processing relies on the interaction between two separable processes, semantic representation and semantic control (Lambon Ralph et al., 2017). The semantic representation system encodes generalisable semantic information across contexts, while the semantic control system manipulates activation within the representation system in specific contexts, focusing on task-relevant knowledge and inhibiting task-irrelevant knowledge (Chiou et al., 2018; Hoffman et al., 2018; Jefferies, 2013; Lambon Ralph et al., 2017). Semantic dementia patients have focal damage to bilateral anterior temporal lobes, resulting in a specific impairment of multimodal semantic representation, rather than semantic control (Jefferies et al., 2008; Jefferies & Lambon Ralph, 2006; Lambon Ralph & Patterson, 2008; Patterson et al., 2007). Therefore, their preserved syntax only demonstrates that syntax is dissociable from semantic representation. Damage to left inferior prefrontal or posterior temporal regions results in an impairment of semantic control, referred to as semantic aphasia (Jefferies & Lambon Ralph, 2006; Thompson et al., 2022). However, the relationship between this impairment and syntactic abilities has not been systematically investigated. Therefore, the relationship between semantic control and syntax remains unclear.

Neuroimaging studies have shown that syntactic and semantic processing recruit overlapping frontal-temporal networks, including the left inferior frontal gyrus (IFG) and posterior temporal cortex (Bautista & Wilson, 2016; Fedorenko et al., 2020; Friederici, 2012; Heim et al., 2008). Syntax is primarily associated with left IFG, posterior superior and middle temporal gyrus (pSTG/MTG), and inferior parietal lobe (IPL) (Friederici et al., 2003; Friederici & Kotz, 2003; Hagoort & Indefrey, 2014; Rodd et al., 2015; Turker et al., 2023; Tyler et al., 2011), while semantic control recruits bilateral IFG (with a preference for the left), left posterior middle and inferior temporal gyrus (pMTG/ITG), and bilateral dorsomedial prefrontal cortex (dmPFC) (Gao et al., 2021; Jackson, 2021; Jefferies, 2013; Noonan et al., 2013; Wang et al., 2018). There may, therefore, be overlap between these neural networks in frontal and temporal cortices, which could reflect shared control processes supporting demanding syntactic and semantic processing. Although the two processes appear to recruit similar regions, dissociations have been reported in the left IPL and IFG. The left IPL is strongly associated with syntactic processing (Lee & Newman, 2010; Tyler et al., 2011), but does not respond reliably to semantic control (Jackson, 2021). In addition, prior work has demonstrated dissociations between anterior left IFG for semantic processing and posterior IFG for syntactic processing (Friederici, 2011; Goucha & Friederici, 2015; Matchin et al., 2022; Schell et al., 2017; Vigneau et al., 2006), although these studies did not consider semantic and syntactic control demands.

The IFG and PTC regions implicated in semantic control are not simply responsible for domain-general executive control. The semantic control network (SCN) is defined based solely on the contribution within the semantic domain, by contrasting more controlled (and harder) semantic cognition over less controlled (and easier) semantic cognition (Jackson, 2021; Jefferies, 2013; Noonan et al., 2013). This contrast does not merely identify the multiple-demand network (MDN) implicated in domain-general executive control (Assem et al., 2020; Camilleri et al., 2018; Duncan, 2010; Fedorenko et al., 2013). While these networks overlap in some areas (e.g., dorsomedial prefrontal cortex), they are largely dissociable. The core regions of the SCN, including left IFG and left posterior temporal cortex, show selectivity for semantic stimuli, responding more for the control of meaningful content, even when task process and difficulty are matched (Chiou et al., 2023; Davey et al., 2016; Diachek et al., 2020; Fedorenko et al., 2024; Gao et al., 2021; Hodgson et al., 2024; Humphreys & Lambon Ralph, 2017). Thus, involvement of SCN regions in demanding syntactic processing would point to a particular role for semantic control, while overlap with MDN would instead suggest a domain-general executive control component.

Formal meta-analyses are needed to systematically identify the relationship between semantic control and syntactic processing, since existing comparisons have not considered subcomponents of semantic cognition (Turker et al., 2023). One exception is Rodd et al. (2015) who contrasted high demands with easier tasks to investigate semantic and syntactic processing across visual and auditory modalities. However, the studies available at the time left these comparisons underpowered (26 semantic and 28 syntactic studies), and they were unable to compare across the two modalities.

In the present study, we aimed to identify the neural correlates of syntactic processing and semantic control to examine two key questions. First, to what extent does demanding syntactic processing recruit regions of the semantic control network versus additional domain-general or syntax-specific areas? Secondly, are the regions engaged by syntactic processing multimodal, responding to both auditory and visual stimuli, and how does this compare with the effects of modality in semantic control regions? To address these questions, we focused on conditions of varying demand in both semantic and syntactic domains, following a novel meta-analytic approach inspired by Rodd et al. (2015). The syntactic contrast was constructed in a manner analogous to standard semantic control contrasts (e.g., Jackson, 2021; Noonan et al., 2013), allowing direct comparison of controlled processing across the two domains. The semantic control meta-analysis (Jackson, 2021) was modified to only include verbal stimuli, allowing direct comparison with syntax. We then examined the overlap of regions implicated in syntactic processing demands with the semantic control network and the multiple-demand network (Fedorenko et al., 2013) to determine whether overlap between syntax and semantic control could be explained by the recruitment of domain-general executive processing regions.

Previous studies have reported multimodal responses in left IFG and posterior temporal cortex for both semantic control and syntactic tasks (Buchweitz et al., 2009; Corbett et al., 2009; Jackson, 2021; Jefferies & Lambon Ralph, 2006), yet the precise relationship between multimodal semantic and syntactic regions remains unclear. Importantly, there is an imbalance in the proportion of visual and auditory studies between syntactic processing and semantic control, with a higher proportion of visual studies in semantic control compared with demanding syntax. Therefore, we distinguished between the visual and auditory modalities. First, this allowed us to examine whether differences between syntactic processing and semantic control might reflect differences in input modality. Second, we aimed to determine whether the multimodal semantic control regions support syntactic processing across both the visual and auditory modalities.

2. METHOD

This meta-analysis was performed and reported following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Moher et al., 2009; Page et al., 2021). The study screening and selection process was performed in Covidence (www.covidence.org), a systematic review software.

2.1. Inclusion and exclusion criteria

2.1.1. Syntactic processing

For syntactic processing, studies were taken from two sources: previous meta-analyses and a new literature search. First, studies identified from previous meta-analyses in syntactic processing (Hagoort & Indefrey, 2014; Heard & Lee, 2020; Rodd et al., 2015; Vigneau et al., 2006, 2011; Zaccarella et al., 2017) were included. While some of these meta-analyses focused on specific operations in syntactic processing (e.g., merge in Zaccarella et al., 2017), others took a broader view. For example, Hagoort and Indefrey (2014) examined semantic and syntactic processing at the sentence level, categorising syntactic manipulations into complexity, violation, and ambiguity. Similarly, Rodd et al. (2015) compared semantic and syntactic processing, encompassing comprehensive syntactic manipulations (i.e., violation, complexity, ambiguity, and cross-modal priming). They used stringent inclusion criteria—excluding studies where contrasts included both syntactic and semantic processing (e.g., sentences vs. word lists, and sentences vs. "jabberwocky" sentences)—to avoid potential confounds between these two domains. These previous meta-analyses covered the literature until 2014. To extend this, we, therefore, conducted a literature search in Web of Science from 2014 to May 2024. To identify as much related literature as possible, we used the search string: (fMRI OR functional magnetic resonance imaging OR PET OR positron emission tomography) AND (syntax OR syntactic OR grammar OR grammatical OR sentence). After removing duplicates from the two sources, 1,400 studies were included in the initial screening.

The initial screening was performed based on titles and abstracts. Studies that did not meet the following inclusion criteria were excluded in this initial screening: (1) peer-reviewed journal articles written in English; (2) empirical studies (not reviews or meta-analyses); (3) task-based fMRI or PET studies; (4) studies focused on healthy young adults (aged 18–50 years), including healthy control groups in patient studies; (5) studies using tasks where syntactic processing was the major cognitive process. After the initial screening stage, 255 studies passed to the second screening stage.

The second screening stage was performed based on the full texts. Studies had to meet the criteria described above, as well as the following criteria: (1) whole-brain coverage; (2) univariate activation analysis without small volume correction; (3) peak coordinates reported in Talairach or Montreal Neurological Institute (MNI) stereotaxic space; (4) stimuli were sentences, word lists, or word pairs in visual or auditory modalities; (5) contrasts were more demanding > less demanding syntactic processing, including ambiguous > unambiguous, complex > simple sentence structures and syntactically incorrect > correct. Studies using low-level references (e.g., fixation, rest, or other non-linguistic stimuli) were excluded, as these involve cognitive processes other than language processing. Moreover, following Rodd et al. (2015), studies where the contrasts resulted in differences in both semantic and syntactic processing (e.g., sentences vs. word lists, and sentences vs. "jabberwocky" sentences) were excluded, to promote the separation of these domains. Thus, all included studies involved syntactic processing as the major cognitive process performed on verbal stimuli and contrasted a more demanding over a less demanding condition. This allowed us to isolate brain regions engaged by syntactic demands. Cross-modal priming studies were not included in the present study. Following Hagoort and Indefrey (2014), studies were further classified into three categories: syntactic violation (e.g., subject–verb disagreement > agreement), ambiguity (e.g., word-class ambiguity), and complexity paradigms (e.g., passive > active sentences, non-canonical > canonical word-order, center-embedding > left/right-branching, object-relative > subject-relative clauses) based on syntactic manipulations. Across these studies, participants performed various tasks to probe syntactic processing, such as passive listening/reading, grammaticality judgement, comprehension/verification, and picture–sentence matching tasks. Multiple contrasts reported for the same participant sample were analysed as a single contrast following the recommendation of Müller et al. (2018).

A total of 66 experiments with 513 foci were included in the formal meta-analysis (Fig. 1). In follow-up analyses, these were divided to compare the 21 experiments (108 foci) in the auditory modality with the 43 experiments

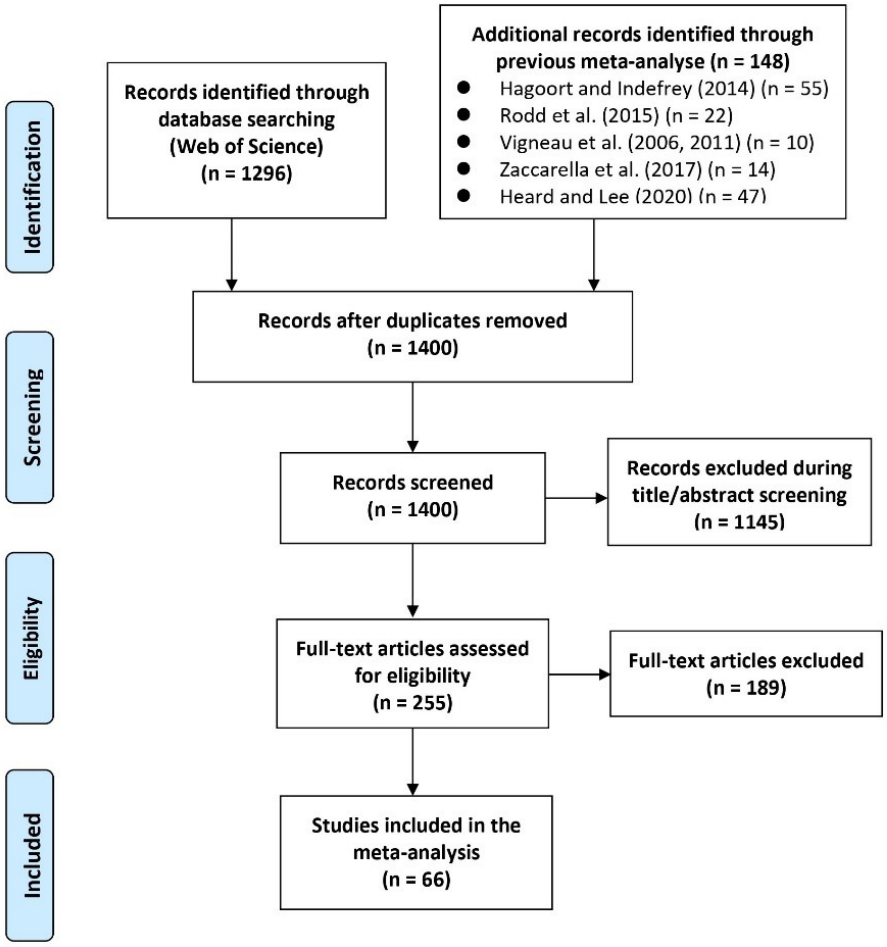


Fig. 1. PRISMA flow chart for syntactic processing.

(371 foci) in the visual modality, and 2 experiments (34 foci) involving both modalities. All 66 experiments were included for the analysis of general syntactic processing, while the 2 experiments involving both modalities were excluded from modality-specific analyses. Additionally, following Hagoort and Indefrey (2014), the particular syntactic manipulation was compared by contrasting the 50 experiments (346 foci) on complexity and 14 experiments (151 foci) on violation. The 2 experiments (16 foci) in ambiguity were not assessed independently, as there was an insufficient number of studies for a meta-analysis (as we utilised stricter inclusion criteria to disambiguate syntax and semantics than prior investigation). All experiments included are described, and the peaks are provided in Supplementary Table S1.

2.1.2. Semantic control

The regions consistently activated for syntactic demands were compared with those implicated in semantic control. For semantic control, we sourced the same studies as a recent meta-analysis on semantic control (Jackson, 2021; see also Hodgson et al., 2023). This meta-analysis contrasted more over less demanding semantic processing across both verbal and nonverbal stimuli in visual and auditory modalities. However, to focus on the language domain, we restricted our analysis to studies using verbal stimuli in both visual and auditory modalities (7 experiments with 46 foci using non-verbal stimuli in visual modality were excluded) and re-ran the meta-analysis, including only the studies using verbal stimuli without further changes. This resulted in a total of 82 experiments with 871 foci, including 65 experiments (712 foci) in the visual modality and 17 experiments (159 foci) in the auditory modality.

2.2. Activation likelihood estimation

The meta-analyses were performed in GingerALE 3.0.2 (https://brainmap.org) using the activation likelihood estimation method (ALE; Eickhoff et al., 2009, 2012, 2017; Turkeltaub et al., 2012). Talairach foci were first converted to MNI standard space using the tal2icbm_spm transformation implemented in GingerALE. All analyses were performed in MNI152 space. The ALE method identifies regions of consistent activation across studies by modelling reported foci as Gaussian probability distributions. First, a model activation map was generated for each experiment, where each activation focus was modelled as a three-dimensional Gaussian probability distribution centred at its reported coordinates. To account for spatial uncertainty, the Gaussian distribution's full-width at half-maximum (FWHM) was adjusted according to each study's sample size (larger sample sizes resulting in smaller FWHM values, indicating greater spatial precision). Next, an ALE map was generated by computing the union of model activation maps across all experiments, resulting in an ALE score for each voxel. This map represents the convergence of activation probabilities across studies, with each voxel's ALE score indicating the likelihood of consistent activation at that location.

Independent ALE analyses were performed to identify the areas consistently involved in syntax and semantic control. ALE scores were thresholded at $p < 0.001$ at the voxel-level and FWE corrected $p < 0.05$ at the cluster-level, with 10,000 permutations (Müller et al., 2018). Contrast and conjunction analyses were conducted on the resulting maps to reveal the distinct and shared neural underpinnings of semantic control and syntactic processing. The conjunction analysis simply identifies any voxels present in both thresholded maps. The contrast analysis identifies regions more likely to activate in one condition over the other by subtracting one thresholded map from the other and assessing whether the resulting differences are significantly larger than would be expected by chance. Contrast scores were thresholded at voxel-level $p < 0.001$ with 10,000 permutations, cluster volume >20 mm^3. The two syntactic manipulations (syntactic complexity and violation) were then analysed separately and compared. Additionally, we examined the pattern of activation for syntax and semantic control in the visual and auditory modalities, and compared these modality-specific patterns (visual vs. auditory syntax and visual vs. auditory semantic control). The regions identified as consistently supporting syntactic demands were also compared with *a priori* network masks for general semantic cognition and domain-general cognitive control, obtained from Jackson (2021) and Fedorenko et al. (2013), respectively. The general semantic cognition mask was previously obtained by contrasting semantic and non-semantic demands, and, therefore, includes areas implicated in semantic representation as well as semantic control. These comparisons allowed quantification of the proportion of syntax regions that overlap semantic control, non-control semantic, and domain-general control regions.

3. RESULTS

3.1. Syntactic processing regions

The regions consistently activated during syntactic processing are shown in Figure 2. Peak coordinates are reported in Table 1. The largest cluster is in the left IFG, including pars opercularis and pars triangularis, extending to the insula and precentral gyrus. The strongest activation likelihood is in pars opercularis. A second cluster

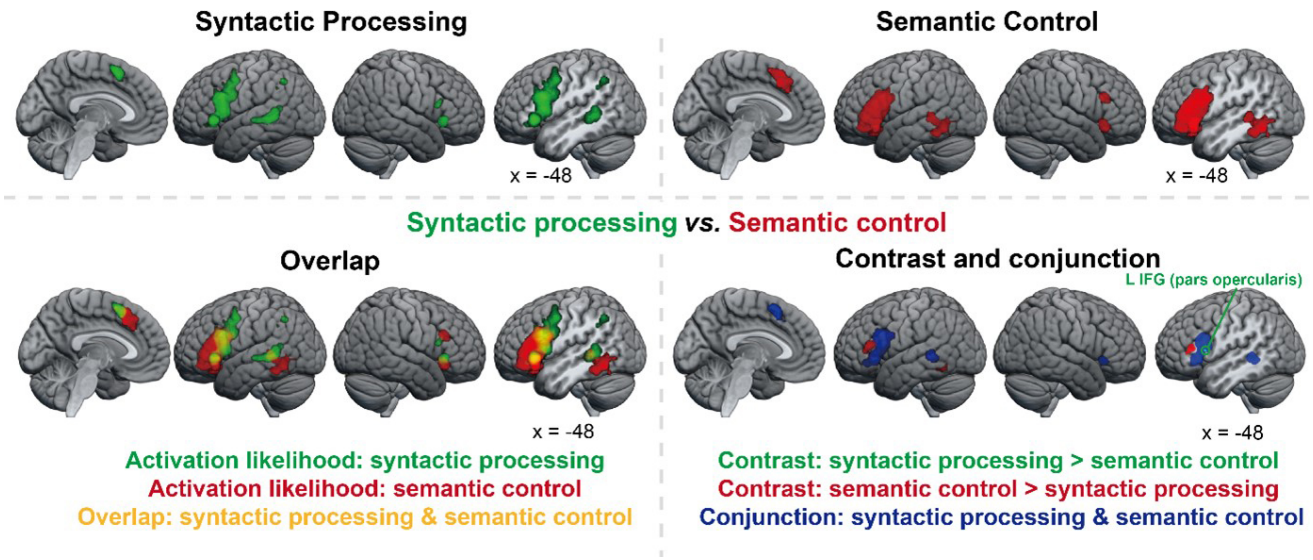


Fig. 2. Top: Activation likelihood estimation maps for syntactic processing (top left, shown in green) and semantic control (top right, shown in red) at a voxel-level $p < 0.001$, cluster-level FWE corrected $p < 0.05$, with 10,000 permutations. Bottom: Overlap of ALE results of syntactic processing and semantic control (bottom left, overlap in yellow). Contrast and conjunction analysis between syntactic processing and semantic control at a voxel-level $p < 0.001$ with 10,000 permutations, cluster volume > 20 mm^3 (bottom right, syntactic processing > semantic control in green, semantic control > syntactic processing in red, conjunction in blue).

is in the left posterior middle and superior temporal gyri, focused on the posterior superior temporal sulcus (pSTS). Additional activations are in the left IPL (including angular gyrus and supramarginal gyrus) and bilateral dmPFC, including supplementary motor area (SMA). Two clusters are identified in the right hemisphere, in the insula and IFG, including pars opercularis and pars triangularis. This result reveals a distributed, left-dominant network for syntactic processing, focused around IFG, dmPFC, and dorsal posterior temporal cortex. Analyses comparing the type of syntactic manipulations are presented in the Supplementary Materials (Supplementary Fig. S1 and Supplementary Table S2) only, as most studies included variation in syntactic complexity, rather than violation or ambiguity. Whether different syntactic manipulations would result in changes to this network should be explored in further work.

3.2. Comparing syntactic processing regions with semantic control

Semantic control also relies upon a distributed left-dominant network with crucial nodes in the left prefrontal and posterior temporal cortices. To directly compare the regions implicated in semantic and syntactic demands, we replicated a recent semantic control meta-analysis, using only the verbal stimuli (Fig. 2 and Table 1). As found previously (Jackson, 2021; Noonan et al., 2013), bilateral IFG, insula, and dmPFC are consistently implicated in semantic control, alongside a left posterior temporal cortex region, covering the lateral surface from the posterior STS, through MTG and ITG into fusiform gyrus.

Directly comparing the regions consistently implicated in the two domains highlighted substantial overlap in left IFG extending to the insula and precentral gyrus, left dmPFC, left pMTG/pSTS, and right insula (see Fig. 2 and Table 2). Formal contrast analyses nevertheless identified some areas of difference. Compared with syntactic processing, semantic control showed greater activation in left dorsal anterior IFG (pars triangularis), as well as posterior fusiform and inferior temporal gyri, and a small cluster in ventral IFG (pars orbitalis). In contrast, syntactic processing showed greater activation in a small region of left IFG (pars opercularis), overlapping the area consistently implicated in both processes.

3.3. Comparing syntactic processing regions with semantic representation and multiple-demand network

Syntactic demands activate the semantic control network, yet this may not be the full picture. Could this overlap be due to general executive processing demands shared across multiple domains? Additionally, can we explain the differences identified between syntactic and semantic demands, albeit in the context of large overlap? Specifically, does demanding syntactic processing recruit semantic regions more generally outside of the SCN, and/or does it rely on additional domain-general cognitive control processes beyond semantic control? We

Table 1. Activation likelihood estimation values for syntactic processing and semantic control.

Cluster number	Region	ALE	Z	Cluster size (mm^3)	Peak MNI Coordinates		
					X	Y	Z
Syntactic processing							
1	L IFG (pars opercularis & triangularis)/ insula/precentral gyrus	0.069	9.211	21496	-52	14	12
		0.047	7.126		-32	26	-2
		0.038	6.111		-42	0	44
		0.034	5.615		-40	6	30
		0.030	5.134		-52	26	2
		0.019	3.718		-50	12	40
2	L pSTS/pMTG/pSTG	0.043	6.659	6136	-56	-42	2
		0.030	5.143		-58	-26	-2
		0.023	4.352		-62	-52	12
3	Bilateral dmPFC	0.046	6.992	3408	-2	16	54
		0.022	4.145		2	22	46
4	L IPL	0.024	4.400	1808	-30	-58	44
		0.018	3.520		-34	-50	36
5	R insula	0.047	7.135	1024	32	24	-4
6	R IFG (pars opercularis & triangularis)	0.026	4.645	888	46	18	16
Semantic control							
1	L IFG (pars triangularis, orbitalis & opercularis)/insula	0.083	9.835	26240	-50	22	20
		0.059	7.714		-46	24	-2
		0.055	7.319		-50	30	0
		0.037	5.453		-34	26	-6
		0.036	5.348		-46	40	-10
		0.034	5.105		-48	34	-12
		0.029	4.530		-30	26	-16
		0.020	3.321		-38	28	-22
2	Bilateral dmPFC	0.049	6.765	6048	-2	20	52
		0.033	5.016		2	28	36
		0.029	4.611		-4	30	44
		0.025	3.997		-4	8	58
3	L pITG/pMTG/fusiform gyrus/pSTS	0.037	5.454	5968	-46	-48	-16
		0.036	5.398		-46	-56	-12
		0.035	5.248		-54	-40	2
		0.034	5.181		-56	-46	-4
		0.021	3.478		-50	-68	-2
		0.020	3.370		-46	-64	-20
4	R IFG (pars orbitalis)/insula	0.046	6.472	2712	32	24	-6
		0.019	3.267		30	18	-18
5	R IFG (pars triangularis)	0.042	6.052	2192	52	24	26

Note: L = left, R = right. IFG = inferior frontal gyrus, p = posterior, STS = superior temporal sulcus, MTG = middle temporal gyrus, STG = superior temporal gyrus, dmPFC = dorsomedial prefrontal cortex, IPL = inferior parietal lobe, ITG = inferior temporal gyrus. Voxel-level $p < 0.001$, cluster-level FWE corrected $p < 0.05$, with 10,000 permutations.

examined the overlap between brain regions involved in demanding syntactic processing and three networks: the SCN (generated above), the multiple-demand network (MDN) responsible for domain-general executive control, and regions supporting general semantic cognition that are not implicated in either form of control (semantic, not SCN/MDN). The MDN mask was generated by Fedorenko et al. (2013), and the general semantic cognition mask was created by Jackson (2021).

Consistent with the demonstration above, demanding syntactic processing mostly fell within the SCN. However, there was additional recruitment of the left dorsal frontal cortices and left IPL, regions within the MDN. A smaller part of the pSTS/pMTG/pSTG fell within the semantic regions not involved in control (Fig. 3). However, this area is within the SCN identified in Jackson (2021), it has simply failed to reach significance in the language-only version of this meta-analysis conducted here. Additionally, it is within the regions thought to cause semantic control impairments when damaged (Jefferies & Lambon Ralph, 2006; Thompson et al., 2018). Moreover, the key regions implicated in semantic cognition,

Table 2. Contrast and conjunction analyses between syntactic processing and semantic control.

Cluster number	Region	Cluster size (mm^3)	Peak MNI coordinates		
			X	Y	Z
Contrast analysis:					
syntactic processing > semantic control					
1	L IFG (pars opercularis)	32	-54	16	10
semantic control > syntactic processing					
1	L IFG (pars triangularis)	1944	-49	32	13
2	L fusiform gyrus/ITG	352	-48	-58	-16
			-52	-60	-10
			-46	-50	-16
3	L IFG (pars orbitalis)	24	-28	32	-18
Conjunction analysis: syntactic processing & semantic control					
1	L IFG (pars opercularis & triangularis)/ insula/precentral gyrus	12328	-52	18	18
			-52	26	0
			-34	26	-4
			-42	6	26
2	L dmPFC	2032	-2	16	54
3	L pMTG/pSTS	1680	-54	-42	2
			-56	-46	-2
4	R insula	912	32	24	-6

Note: L = left, R = right. IFG = inferior frontal gyrus, ITG = inferior temporal gyrus, dmPFC = dorsomedial prefrontal cortex, p = posterior, MTG = middle temporal gyrus, STS = superior temporal sulcus. Voxel-level $p < 0.001$ with 10,000 permutations, cluster volume > 20 mm^3.

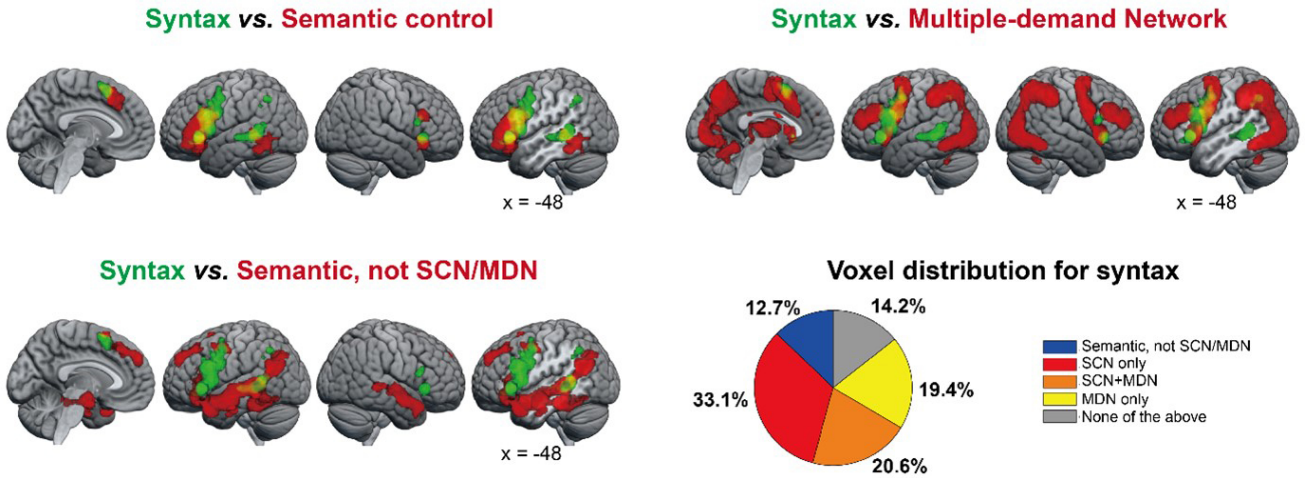


Fig. 3. Top, left: overlap between syntax (green) and semantic control (red). Overlap shown in yellow. Top, right: syntax (green) in the context of multiple-demand network (MDN) mask generated in Fedorenko et al., 2013 (red). Overlap shown in yellow. Bottom, left: overlap between syntax (green) and general semantic cognition not implicated in the semantic control network (SCN) or MDN (semantic, not SCN/MDN, red). The general semantic cognition mask was generated in Jackson (2021). Overlap shown in yellow. Bottom, right: voxel distribution of the syntax result within (i) the SCN not implicated in the MDN, (ii) the MDN not implicated in the SCN, (iii) the overlap of the SCN and MDN, (iv) semantic not SCN/MDN. Voxels outside these networks are also shown (none of the above). The syntax result included a total of 4345 voxels.

yet not semantic control, such as the ATL and ventral angular gyrus, were not reliably activated for syntactic demands. Of the total 5395 SCN voxels, 34% also fall within the large MDN mask (including 28761 voxels). We dissociated regions shared between the SCN and MDN from regions specific to the SCN or the MDN. Overall, 33.1% of syntactic regions fell within the SCN alone, 20.6% of syntactic regions fell within the regions shared between the SCN and MDN, 19.4% within the MDN not implicated in the SCN, and 12.7% within the semantic, not SCN/MDN regions (4345 voxels in total, Fig. 3). Despite the larger size of the MDN mask, there was more evidence for overlap between demanding syntax and semantic control regions. Moreover, the results particu-

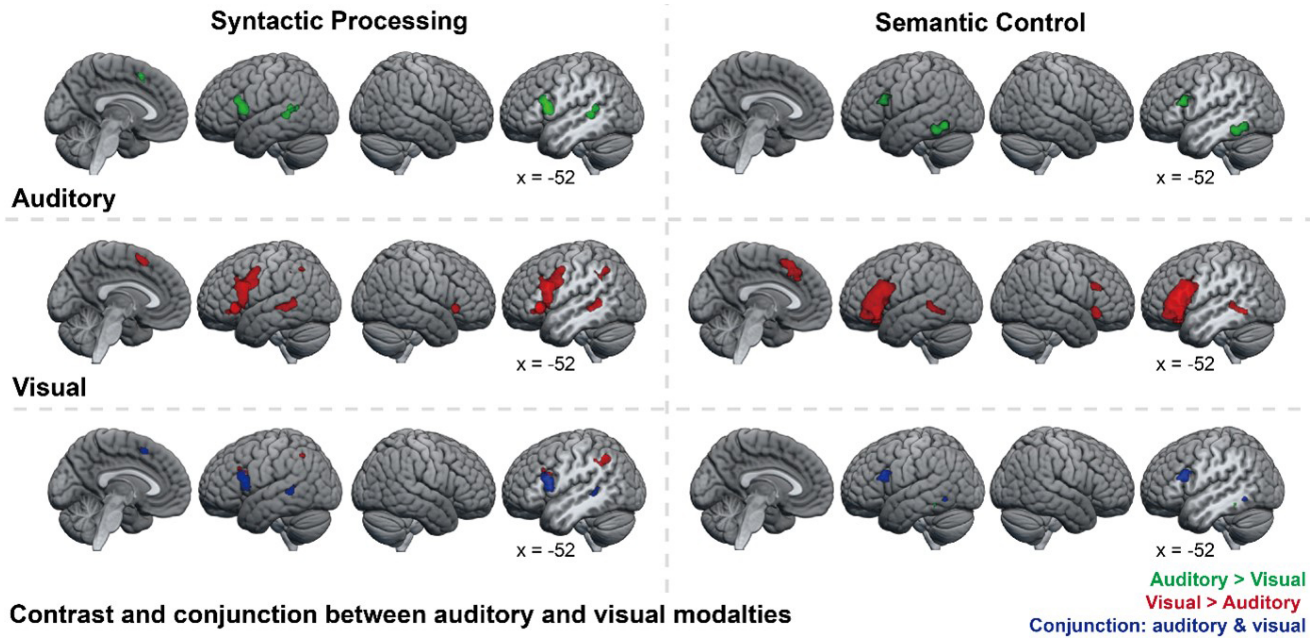


Fig. 4. Top row: Activation likelihood estimation maps for auditory syntactic processing (left) and auditory semantic control (right). Second row: Activation likelihood estimation maps for visual syntactic processing (left) and visual semantic control (right). Bottom row: Contrast and conjunction analyses between auditory and visual modalities for syntactic processing (left) and semantic control (right), with auditory > visual in green, visual > auditory in red, and the conjunction of auditory and visual modalities in blue.

larly implicated the left IFG and PTC regions functionally specialised for semantic control.

3.4. Syntactic processing and semantic control regions in visual and auditory modalities

Next, we asked whether the effect of input modality is the same for syntax and semantic control. More studies involved visual presentation for both syntactic and semantic control, although this difference was greater for semantic control. Indeed, visual syntactic processing recruited a similar network to general syntactic processing, while auditory syntactic processing identified more circumscribed regions of left IFG (pars triangularis and pars opercularis), left pMTG/pSTS, and dmPFC (Fig. 4 and Table 3), which were shared with the visual condition. Compared with auditory syntactic processing, visual syntactic processing showed greater activation in the left IPL and left IFG (pars triangularis and pars opercularis) extending to MFG (Fig. 4 and Table 4).

We replicated the separation of semantic control conditions into auditory verbal and visual verbal stimuli from Jackson's (2021) meta-analysis. As a greater number of studies were visual, more of the SCN was identified for visual than for auditory semantic control (see Fig. 4 and Table 3). The two modalities shared activation in the left prefrontal and posterior temporal cortex (IFG and pITG) (Fig. 4 and Table 4), supporting the multimodal nature of these core semantic control regions. Despite this, significantly greater involvement was identified for a small region of pITG for auditory semantic control.

Overall, both semantic control and syntactic processing were supported by modality-general regions of the inferior frontal and posterior temporal cortex. Although increasing syntactic demands for visually presented stimuli may also recruit modality-specific regions outside of (or on the edge of) semantic control areas, including inferior parietal cortex and posterior IFG, the core regions supporting demanding syntactic processing overlapped with multimodal SCN. For both domains, the spatial extent of the visual network was larger than that of the auditory network, likely due to the smaller number of studies using auditory stimuli.

4. DISCUSSION

Prior assessments of the brain regions engaged by semantic cognition and syntax fail to consider the crucial separation between semantic representation and control. This study used formal meta-analyses to identify whether demanding syntactic processing recruits the semantic control network. Remarkably, demanding syntactic processing engaged every region of the distributed SCN with the same pattern of lateralisation as semantic control, including IFG (in both hemispheres, yet particularly on the left), bilateral dmPFC, and left lateral posterior

Table 3. Activation likelihood estimation values for syntactic processing and semantic control in visual and auditory modalities.

Cluster number	Region	ALE	Z	Cluster size (mm^3)	Peak MNI coordinates		
					X	Y	Z
Auditory syntactic processing							
1	L IFG (pars opercularis & triangularis)	0.026	6.080	4176	-52	12	12
		0.019	5.031		-52	20	22
2	L pMTG/pSTG/pSTS	0.020	5.142	2744	-54	-42	2
		0.018	4.852		-48	-46	12
		0.014	4.139		-62	-46	8
		0.014	4.053		-62	-54	12
3	L dmPFC	0.014	4.166	744	-2	16	52
Visual syntactic processing							
1	L IFG (pars triangularis & opercularis)/ insula/precentral gyrus	0.041	6.897	17056	-40	14	26
		0.040	6.774		-54	16	12
		0.040	6.732		-32	26	-2
		0.037	6.400		-48	16	20
		0.035	6.158		-40	2	44
		0.032	5.793		-40	4	30
		0.026	5.066		-46	26	-6
		0.018	3.904		-48	34	-8
2	L pMTG/pSTS	0.026	5.098	3104	-54	-48	4
		0.026	5.039		-56	-36	-2
3	L dmPFC	0.031	5.703	2032	-2	16	54
4	L IPL	0.024	4.713	1728	-30	-58	44
		0.018	3.842		-34	-50	36
		0.015	3.495		-40	-44	42
5	R insula	0.038	6.530	1464	32	24	-2
Auditory semantic control							
1	L pITG/fusiform gyrus	0.024	5.695	2440	-46	-46	-18
		0.022	5.348		-46	-56	-12
2	L IFG (pars triangularis & opercularis)	0.018	4.772	1544	-52	20	18
Visual semantic control							
1	L IFG (pars triangularis, orbitalis & opercularis)/insula	0.068	8.874	25272	-48	24	20
		0.059	8.018		-48	30	12
		0.055	7.616		-46	24	-2
		0.033	5.329		-34	26	-6
		0.032	5.163		-44	42	-10
		0.031	5.008		-48	32	-12
		0.028	4.675		-30	26	-16
		0.019	3.516		-38	28	-22
		0.018	3.341		-50	10	36
2	Bilateral dmPFC	0.043	6.447	5064	-2	22	52
		0.031	4.999		2	28	36
		0.026	4.414		-8	20	42
		0.025	4.326		-4	32	44
3	L pMTG/pITG	0.031	5.071	2408	-56	-46	-2
4	R IFG (pars orbitalis)/insula	0.038	5.898	2272	32	24	-6
5	R IFG (pars triangularis)	0.033	5.308	1768	52	26	24
		0.017	3.243		48	32	14

Note: L = left, R = right. IFG = inferior frontal gyrus, p = posterior, MTG = middle temporal gyrus, STG = superior temporal gyrus, STS = superior temporal sulcus, dmPFC = dorsomedial prefrontal cortex, IPL = inferior parietal lobe, ITG = inferior temporal gyrus. Voxel-level $p < 0.001$, cluster-level FWE corrected $p < 0.05$, with 10,000 permutations.

Table 4. Contrast and conjunction analyses between auditory and visual modalities.

Cluster number	Region	Cluster size (mm^3)	Peak MNI coordinates		
			X	Y	Z
Syntactic processing:					
Auditory syntactic processing > visual syntactic processing					
No significant results					
Visual syntactic processing > auditory syntactic processing					
1	L IPL	1328	-33	-56	45
			-37	-52	36
2	L IFG (pars triangularis & opercularis)/ MFG	288	-42	24	32
			-37	15	26
			-36	10	24
Conjunction of auditory syntactic processing & visual syntactic processing					
1	L IFG (pars opercularis & triangularis)	3032	-52	12	12
			-52	20	22
2	L pMTG/pSTS	784	-54	-42	2
			-50	-46	8
3	L dmPFC	496	-2	16	52
Semantic control:					
Auditory semantic control > visual semantic control					
1	L pITG/fusiform gyrus	56	-43	-44	-15
Visual semantic control > auditory semantic control					
No significant results					
Conjunction of auditory semantic control & visual semantic control					
1	L IFG (pars triangularis & opercularis)	1528	-52	20	18
2	L pITG	120	-48	-58	-10

Note: L =left, R = right. IPL = inferior parietal lobe, IFG = inferior frontal gyrus, MFG = middle frontal gyrus, p = posterior, MTG = middle temporal gyrus, STS = superior temporal sulcus, dmPFC = dorsomedial prefrontal cortex, ITG = inferior temporal gyrus. Voxel-level $p < 0.001$ with 10,000 permutations, cluster volume > 20 mm^3.

temporal cortex. Substantial overlap can be seen across the left IFG and posterior temporal cortex regions known to be necessary for semantic control (Jefferies & Lambon Ralph, 2006; Thompson et al., 2022). In contrast, key semantic areas outside the semantic control network were not recruited.

Despite this overlap, direct contrasts revealed some distinctions between the regions engaged by the two processes. There was a greater likelihood of activation for the anterior aspects of IFG and the posterior ITG for semantic control than demanding syntax. No regions outside of the SCN showed greater activation likelihood for demanding syntax than semantic control. However, a small cluster within the posterior IFG, bordering the precentral gyrus, did show this pattern. Additionally, demanding syntax consistently recruited a left IPL region, and the lateral frontal cluster extended more dorsally, although these regions were not identified as significantly more active in the contrast analysis.

Like controlled semantic processing, demanding syntactic processing engaged SCN regions irrespective of the modality of presentation (written versus spoken words). Yet unlike semantic control, demanding syntax also demonstrated modality-specific responses, with greater activation likelihood for visual than for auditory stimuli in dorsal IFG/MFG and IPL. Importantly, the core SCN regions in inferior frontal and posterior temporal cortex were engaged across both modalities. Thus, controlled processing of syntax appears to engage the multimodal SCN, perhaps as well as additional regions associated with domain-general executive control, particularly for visually presented stimuli. Our findings suggest that the comparison between demanding syntactic processing and semantic control is not driven by differences in input modalities. Instead, core SCN regions were engaged in demanding syntactic processing regardless of the input modality, consistent with the evidence that the multimodal SCN supports semantic control.

The present study also considers the association between syntax and distinct components of semantic cognition: we separately visualised the overlap between demanding syntax and semantic control and the overlap between syntax and semantic regions not implicated in control. The overlap between syntax and semantics was strongly focused on the distributed SCN. The overlap identified within the pSTS/MTG may reflect control or language-related processes (Hickok & Poeppel, 2007; Hodgson et al., 2024; Jackson, 2021) but is not a key

area for representing semantic content. Semantic representation areas, including the multimodal anterior temporal lobe (ATL) hub, were not implicated in demanding syntactic processing. This is consistent with the preservation of syntax in semantic dementia (Landin-Romero et al., 2016; Rochon et al., 2004). By separating semantic cognition into semantic control and representation components, we are able to explain both prior associations and dissociations with syntax in a systematic fashion (Hagoort & Indefrey, 2014; Rodd et al., 2015; Turker et al., 2023; Vigneau et al., 2006, 2011). Maintaining a separation between semantic representations and syntax allows orthogonal manipulation of meaning and sentence structure, for instance, enabling novel sentences to be easily generated when new vocabulary is learnt. Yet, the SCN acts as a shared resource to support both demanding syntactic and semantic processing.

Why does demanding syntax engage the SCN? One possibility is methodological: some apparent semantic control effects may reflect incidental engagement of syntactic processes, since sentences are occasionally used as stimuli in semantic control studies. In addition, in many syntactic models, words are treated as inputs to syntactic computation, rather than purely semantic units. Therefore, semantic and syntactic processing are intertwined and difficult to dissociate in neuroimaging studies. Indeed, some semantic control manipulations, such as a semantically ambiguous sentence, may require a greater focus on the syntactic structure (Matchin et al., 2023). However, this interpretation appears less likely when considering the multimodal nature of semantic control. The semantic control network responds to both verbal and non-verbal stimuli (Canini et al., 2016; Corbett et al., 2009, 2011; Krieger-Redwood et al., 2015), while syntactic processing is verbal only by definition. Moreover, many semantic control tasks use single words that lack syntactic structure, yet the same regions remain critical (e.g., Satpute et al., 2014; Whitney et al., 2011) and the pattern of impairment in semantic aphasia cannot be explained based on syntactic deficits (Jefferies & Lambon Ralph, 2006; Thompson & Jefferies, 2013; Thompson et al., 2022). Therefore, it is unlikely that regions implicated in semantic control reflect the engagement of syntactic processing alone. In addition, manipulations with large variations in both syntax and semantics, such as comparing sentences vs. word lists or sentences vs. "jabberwocky" sentences, are commonly utilised for syntactic comparisons, yet were excluded from the present meta-analysis to reduce the semantic confounds. Taken together, these considerations suggest that it is unlikely that engagement of the semantic control network primarily reflects syntactic processing. A more compelling account is that demanding syntactic and semantic tasks share a common computational goal—namely, deriving context-sensitive meaning. The function of syntax itself may be to constrain and clarify possible interpretations, such as distinguishing whether *the cat chased the dog* or *the dog chased the cat*. When syntactic complexity increases, semantic prediction becomes less reliable, requiring active resolution among competing interpretations. This selective retrieval and inhibition of context-appropriate versus inappropriate meanings is the hallmark of semantic control (Chiou et al., 2018; Jefferies, 2013; Lambon Ralph et al., 2017). Consequently, both syntactic and semantic challenges may engage overlapping SCN regions because each demands the extraction and integration of meaning that is flexible yet contextually constrained.

While demanding syntactic processing engaged the SCN, consistent activity was also found in IPL and more dorsal frontal cortices. This aligns with a previous meta-analysis showing higher activation likelihood for demanding syntax than demanding semantics (i.e., semantic control) in the left IPL (Rodd et al., 2015). Lesion mapping work has also shown that syntactic comprehension deficits in aphasia are more strongly associated with damage to left temporoparietal cortex (Matchin et al., 2023, 2024). Additionally, a posterior IFG region bordering the precentral gyrus showed greater involvement for syntax. This finding contributes to an ongoing debate on the dissociation between syntax and semantics within the IFG. While some studies have argued against a reliable dissociation in this region (e.g., Siegelman et al., 2019), earlier work reported that the posterior IFG (pars opercularis) is more responsive to syntactic processing, while the anterior IFG (pars orbitalis) shows a greater response for semantic processing (Dapretto & Bookheimer, 1999). Using formal meta-analysis, our study provides evidence for a partial dissociation: while a large cluster in the left IFG was implicated in both semantic and syntactic processing, greater semantic control involvement was identified in anterior and ventral IFG (pars orbitalis), with a small cluster in dorsal and posterior IFG (pars opercularis) appearing more responsive to syntactic processing. Notably, these regions with additional involvement in syntactic processing are not uniquely associated with syntax, but form part of the MDN. While the parietal cortex is not reliably activated across studies of semantic control (Jackson, 2021), inferior parietal cortex is a core region of the MDN (Assem et al., 2020; Fedorenko et al., 2013), and the domain-general precentral gyrus and dorsolateral prefrontal cortex surround the semantic IFG. MDN engagement for demanding syntax would not be surprising, given the network's role in demanding processing across domains. This converging evidence suggests that, in addition to

the SCN, demanding syntax also engages some regions of the MDN.

The presence of meaningful stimuli typically down-regulates activity in the MDN while increasing engagement of the SCN (Hodgson et al., 2024). These networks support distinct forms of control: the SCN facilitates context-sensitive retrieval and selection of meaning, whereas the MDN supports domain-general executive demands such as maintaining and manipulating information in working memory (Gao et al., 2021). The present results suggest that demanding syntactic processing draws on both forms of control. Complex syntactic structures not only require context-sensitive interpretation, invoking the SCN, but also place heavier demands on working memory, engaging elements of the MDN. Consistent with this, tasks emphasising phonological rather than semantic control preferentially recruit the MDN (Hodgson et al., 2021; Noonan et al., 2013). Demanding syntax may, therefore, co-activate SCN regions needed to manage meaning and MDN systems that support structural integration of the elements of a sentence. Importantly, we found no evidence for additional, syntax-specific regions beyond these established control networks.

The SCN showed equivalent responses to visual and auditory stimuli whether performing demanding syntactic or semantic processing. Indeed, semantic aphasia patients have deficits across both visual and auditory semantic control (Thompson & Jefferies, 2013). In addition, demanding syntax showed modality-specific responses in MDN regions, including left dorsal IFG/MFG and IPL. These regions showed a greater activation likelihood for visual than for auditory stimuli. One possible explanation is a visual preference within the MDN. Previous studies have demonstrated sensory biases within the MDN, including a visually biased region in the left inferior precentral sulcus bordering IFG and MFG (Assem et al., 2022; Mayer et al., 2017; Noyce et al., 2017; Tobyne et al., 2017). An alternative explanation is that these differences could arise from participants re-reading the visual stimuli to aid comprehension, while auditory stimuli are fleeting and cannot be revisited. Another possible explanation is that studies assessing syntax visually may use more complex stimuli or more demanding tasks requiring more active judgements than auditory assessments, potentially due to differences in the working memory demands.

It should be noted that our work contrasted more demanding with less demanding syntactic processing to match the semantic control contrast used in this study. Therefore, our findings primarily reflect "syntactic control." There could be additional regions supporting other aspects of syntactic processing which would not be detected here, and these areas may overlap with non-control semantic regions. However, this seems less likely given lesion studies showing at least a partial dissociation between syntax and semantics, with preserved syntax and impaired semantics in semantic dementia patients (Landin-Romero et al., 2016; Rochon et al., 2004), and relatively preserved semantics and impaired syntax in agrammatic stroke and PPA patients (Bonner et al., 2010). Alternatively, such additional areas could fall outside the semantic network and be more specific to syntactic processing. While this appears more likely, the syntactic processing areas identified in previous studies, including the IFG, MFG, and posterior temporal cortex, are largely consistent with the regions identified in our meta-analysis (Fedorenko et al., 2024; Hagoort & Indefrey, 2014; Vigneau et al., 2006, 2011), providing no clear evidence for missed syntactic areas. Moreover, the existence of additional regions would not change the principal conclusion of this work that syntactic processing relies on the semantic control network.

Finally, we consider what this means for the definition of the semantic control network. If it is engaged for both semantic and syntactic processing, is the semantic control network simply a "language control network" responding to any increase in language processing demands? Indeed, semantic control regions may overlap some areas of the proposed Language Network (Fedorenko et al., 2024), within lateral frontal and temporal cortices, albeit without the additional regions responsible for phonology, semantic representation, etc. While this may appear an efficient explanation of the current findings, it does not fit the wider literature on the semantic control network. Firstly, the semantic control network is multimodal and responds to both verbal and non-verbal stimuli (Canini et al., 2016; Corbett et al., 2009, 2011; Krieger-Redwood et al., 2015) as well as controlled episodic processing (Stampacchia et al., 2018, 2019), therefore, language is not necessary to recruit the SCN. In addition, highly demanding phonology and verbal working memory does not recruit the SCN, instead, relying upon the MDN (Gao et al., 2022; Hodgson et al., 2021; Krieger-Redwood et al., 2015; Noonan et al., 2013). Since control over language is neither sufficient nor necessary to recruit the SCN, this network cannot be understood as a general language network.

In conclusion, the present study used formal meta-analysis to demonstrate that syntactic processing relies on the semantic control network, encompassing left-dominant frontotemporal regions including IFG, insula, left posterior temporal cortex, and bilateral dmPFC. Beyond the SCN, demanding syntactic processing may recruit additional regions within the multiple-demand network (MDN), including the left posterior IFG and left IPL,

yet such processing is distinct from core semantic representation areas. Furthermore, for demanding syntax, SCN regions showed multimodal responses to both visual and auditory stimuli, whereas MDN regions (i.e., left IFG/MFG and left IPL) showed a greater activation likelihood for visual than auditory stimuli. Dissociating semantic control and representation is crucial to understand the relationship between semantic cognition and syntax.

DATA AND CODE AVAILABILITY

All data are provided in the Supplementary Materials, and the syntax meta-analysis results are available online at https://github.com/QianwenChang/Syntax_SemanticControl_Meta.

AUTHOR CONTRIBUTIONS

Qianwen Chang: Conceptualisation, investigation, formal analysis, data curation, visualisation, writing—original draft. Beth Jefferies: Conceptualisation, methodology, supervision, writing—review and editing. Rebecca L. Jackson: Conceptualisation, methodology, supervision, writing—review and editing.

DECLARATION OF COMPETING INTEREST

The authors have no competing interests to declare.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available with the online version here: https://doi.org/10.1162/IMAG.a.1281#supplementary-data

REFERENCES

Arana, S., Pesnot Lerousseau, J., & Hagoort, P. (2024). Deep learning models to study sentence comprehension in the human brain. *Language, Cognition and Neuroscience*, *39*(8), 972–990. https://doi.org/10.1080/23273798.2023.2198245

Assem, M., Glasser, M. F., Van Essen, D. C., & Duncan, J. (2020). A domain-general cognitive core defined in multimodally parcellated human cortex. *Cerebral Cortex*, *30*(8), 4361–4380. https://doi.org/10.1093/cercor/bhaa023

Assem, M., Shashidhara, S., Glasser, M. F., & Duncan, J. (2022). Precise topology of adjacent domain-general and sensory-biased regions in the human brain. *Cerebral Cortex*, *32*(12), 2521–2537. https://doi.org/10.1093/cercor/bhab362

Bautista, A., & Wilson, S. M. (2016). Neural responses to grammatically and lexically degraded speech. *Language, Cognition and Neuroscience*, *31*(4), 567–574. https://doi.org/10.1080/23273798.2015.1123281

Bonner, M. F., Ash, S., & Grossman, M. (2010). The new classification of primary progressive aphasia into semantic, logopenic, or nonfluent/agrammatic variants. *Current Neurology and Neuroscience Reports*, *10*(6), 484–490. https://doi.org/10.1007/s11910-010-0140-4

Buchweitz, A., Mason, R. A., Tomitch, L. M. B., & Just, M. A. (2009). Brain activation for reading and listening comprehension: An fMRI study of modality effects and individual differences in language comprehension. *Psychology & Neuroscience*, *2*(2), 111–123. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3081613/

Camilleri, J. A., Müller, V. I., Fox, P., Laird, A. R., Hoffstaedter, F., Kalenscher, T., & Eickhoff, S. B. (2018). Definition and characterization of an extended multiple-demand network. *NeuroImage*, *165*, 138–147. https://doi.org/10.1016/j.neuroimage.2017.10.020

Canini, M., Della Rosa, P. A., Catricalà, E., Strijkers, K., Branzi, F. M., Costa, A., & Abutalebi, J. (2016). Semantic interference and its control: A functional neuroimaging and connectivity study. *Human Brain Mapping*, *37*(11), 4179–4196. https://doi.org/10.1002/hbm.23304

Casilio, M., Rising, K., Beeson, P. M., Bunton, K., & Wilson, S. M. (2019). Auditory-perceptual rating of connected speech in aphasia. *American Journal of Speech-Language Pathology*, *28*(2), 550–568. https://doi.org/10.1044/2018_AJSLP-18-0192

Chiou, R., Humphreys, G. F., Jung, J., & Lambon Ralph, M. A. (2018). Controlled semantic cognition relies upon dynamic and flexible interactions between the executive 'semantic control' and hub-and-spoke 'semantic representation' systems. *Cortex*, *103*, 100–116. https://doi.org/10.1016/j.cortex.2018.02.018

Chiou, R., Jefferies, E., Duncan, J., Humphreys, G. F., & Lambon Ralph, M. A. (2023). A middle ground where executive control meets semantics: The neural substrates of semantic control are topographically sandwiched between the multiple-demand and default-mode systems. *Cerebral Cortex*, *33*(8), 4512–4526. https://doi.org/10.1093/cercor/bhac358

Chomsky, N. (1957). *Syntactic structures*. De Gruyter Mouton. https://doi.org/10.1515/9783112316009

Contreras Kallens, P., Kristensen-McLachlan, R. D., & Christiansen, M. H. (2023). Large language models demonstrate the potential of statistical learning in language. *Cognitive Science*, *47*(3), e13256. https://doi.org/10.1111/cogs.13256

Corbett, F., Jefferies, E., & Lambon Ralph, M. A. (2009). Exploring multimodal semantic control impairments in semantic aphasia: Evidence from naturalistic object use. *Neuropsychologia*, *47*(13), 2721–2731. https://doi.org/10.1016/j.neuropsychologia.2009.05.020

Corbett, F., Jefferies, E., & Lambon Ralph, M. A. (2011). Deregulated semantic cognition follows prefrontal and temporo-parietal damage: Evidence from the impact of task constraint on nonverbal object use. *Journal of Cognitive Neuroscience*, *23*(5), 1125–1135. https://doi.org/10.1162/jocn.2010.21539

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, *24*(2), 427–432. https://doi.org/10.1016/S0896-6273(00)80855-7

Davey, J., Thompson, H. E., Hallam, G., Karapanagiotidis, T., Murphy, C., De Caso, I., Krieger-Redwood, K., Bernhardt, B. C., Smallwood, J., & Jefferies, E. (2016). Exploring the role of the posterior middle temporal gyrus in semantic cognition: Integration of anterior temporal lobe with executive processes. *NeuroImage*, *137*, 165–177. https://doi.org/10.1016/j.neuroimage.2016.05.051

Diachek, E., Blank, I., Siegelman, M., Affourtit, J., & Fedorenko, E. (2020). The domain-general multiple

demand (MD) network does not support core aspects of language comprehension: A large-scale fMRI investigation. *Journal of Neuroscience*, *40*(23), 4536–4550. https://doi.org/10.1523/JNEUROSCI.2036-19.2020

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, *14*(4), 172–179. https://doi.org/10.1016/j.tics.2010.01.004

Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *NeuroImage*, *59*(3), 2349–2361. https://doi.org/10.1016/j.neuroimage.2011.09.017

Eickhoff, S. B., Laird, A. R., Fox, P. M., Lancaster, J. L., & Fox, P. T. (2017). Implementation errors in the GingerALE Software: Description and recommendations. *Human Brain Mapping*, *38*(1), 7–11. https://doi.org/10.1002/hbm.23342

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, *30*(9), 2907–2926. https://doi.org/10.1002/hbm.20718

Fedorenko, E., Blank, I. A., Siegelman, M., & Mineroff, Z. (2020). Lack of selectivity for syntax relative to word meanings throughout the language network. *Cognition*, *203*, 104348. https://doi.org/10.1016/j.cognition.2020.104348

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*, *110*(41), 16616–16621. https://doi.org/10.1073/pnas.1315235110

Fedorenko, E., Ivanova, A. A., & Regev, T. I. (2024). The language network as a natural kind within the broader landscape of the human brain. *Nature Reviews Neuroscience*, *25*(5), 289–312. https://doi.org/10.1038/s41583-024-00802-4

Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, *91*(4), 1357–1392. https://doi.org/10.1152/physrev.00006.2011

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, *16*(5), 262–268. https://doi.org/10.1016/j.tics.2012.04.001

Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: Functional imaging and lesion studies. *NeuroImage, Convergence and Divergence of Lesion Studies and Functional Imaging of Cognition*, *20*, S8–S17. https://doi.org/10.1016/j.neuroimage.2003.09.003

Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, *13*(2), 170–177. https://doi.org/10.1093/cercor/13.2.170

Friederici, A. D., & Weissenborn, J. (2007). Mapping sentence form onto meaning: The syntax–semantic interface. *Brain Research, Mysteries of Meaning*, *1146*, 50–58. https://doi.org/10.1016/j.brainres.2006.08.038

Gao, Z., Zheng, L., Chiou, R., Gouws, A., Krieger-Redwood, K., Wang, X., Varga, D., Lambon Ralph, M. A., Smallwood, J., & Jefferies, E. (2021). Distinct and common neural coding of semantic and non-semantic control demands. *NeuroImage*, *236*, 118230. https://doi.org/10.1016/j.neuroimage.2021.118230

Gao, Z., Zheng, L., Gouws, A., Krieger-Redwood, K., Wang, X., Varga, D., Smallwood, J., & Jefferies, E. (2022). Context free and context-dependent conceptual representation in the brain. *Cerebral Cortex*, *33*(1), 152–166. https://doi.org/10.1093/cercor/bhac058

Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca's Area. *NeuroImage*, *114*, 294–302. https://doi.org/10.1016/j.neuroimage.2015.04.011

Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annual Review of Neuroscience*, *37*(1), 347–362. https://doi.org/10.1146/annurev-neuro-071013-013847

Heard, M., & Lee, Y. S. (2020). Shared neural resources of rhythm and syntax: An ALE meta-analysis. *Neuropsychologia*, *137*, 107284. https://doi.org/10.1016/j.neuropsychologia.2019.107284

Heim, S., Eickhoff, S. B., & Amunts, K. (2008). Specialisation in Broca's region for semantic, phonological, and syntactic fluency? *NeuroImage*, *40*(3), 1362–1368. https://doi.org/10.1016/j.neuroimage.2008.01.009

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393–402. https://doi.org/10.1038/nrn2113

Hodgson, V. J., Lambon Ralph, M. A., & Jackson, R. L. (2021). Multiple dimensions underlying the functional organization of the language network. *NeuroImage*, *241*, 118444. https://doi.org/10.1016/j.neuroimage.2021.118444

Hodgson, V. J., Lambon Ralph, M. A., & Jackson, R. L. (2023). The cross-domain functional organization of posterior lateral temporal cortex: Insights from ALE meta-analyses of 7 cognitive domains spanning 12,000 participants. *Cerebral Cortex*, *33*(8), 4990–5006. https://doi.org/10.1093/cercor/bhac394

Hodgson, V. J., Ralph, M. A. L., & Jackson, R. L. (2024). Disentangling the neural correlates of semantic and domain-general control: The roles of stimulus domain and task process. *Imaging Neuroscience*, *2*, imag–2–00092. https://doi.org/10.1162/imag_a_00092

Hoffman, P., McClelland, J. L., & Lambon Ralph, M. A. (2018). Concepts, control, and context: A connectionist account of normal and disordered semantic cognition. *Psychological Review*, *125*(3), 293–328. https://doi.org/10.1037/rev0000094

Humphreys, G. F., & Lambon Ralph, M. A. (2017). Mapping domain-selective and counterpointed domain-general higher cognitive functions in the lateral parietal cortex: Evidence from fMRI comparisons of difficulty-varying semantic versus visuo-spatial tasks, and functional connectivity analyses. *Cerebral Cortex*, *27*(8), 4199–4212. https://doi.org/10.1093/cercor/bhx107

Jackson, R. L. (2021). The neural correlates of semantic control revisited. *NeuroImage*, *224*, 117444. https://doi.org/10.1016/j.neuroimage.2020.117444

Jefferies, E. (2013). The neural basis of semantic cognition: Converging evidence from neuropsychology, neuroimaging and TMS. *Cortex*, *49*(3), 611–625. https://doi.org/10.1016/j.cortex.2012.10.008

Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. *Brain: A Journal of Neurology*, *129*(Pt 8), 2132–2147. https://doi.org/10.1093/brain/awl153

Jefferies, E., Patterson, K., & Ralph, M. A. L. (2008). Deficits of knowledge versus executive control in

semantic cognition: Insights from cued naming. *Neuropsychologia*, *46*(2), 649–658. https://doi.org/10.1016/j.neuropsychologia.2007.09.007

Kako, E., & Wagner, L. (2001). The semantics of syntactic structures. *Trends in Cognitive Sciences*, *5*(3), 102–108. https://doi.org/10.1016/S1364-6613(00)01594-1

Krieger-Redwood, K., Teige, C., Davey, J., Hymers, M., & Jefferies, E. (2015). Conceptual control across modalities: Graded specialisation for pictures and words in inferior frontal and posterior temporal cortex. *Neuropsychologia, Special Issue: Semantic Cognition*, *76*, 92–107. https://doi.org/10.1016/j.neuropsychologia.2015.02.030

Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, *18*(1), 42–55. https://doi.org/10.1038/nrn.2016.150

Lambon Ralph, M. A., & Patterson, K. (2008). Generalization and differentiation in semantic memory. *Annals of the New York Academy of Sciences*, *1124*(1), 61–76. https://doi.org/10.1196/annals.1440.006

Landin-Romero, R., Tan, R., Hodges, J. R., & Kumfor, F. (2016). An update on semantic dementia: Genetics, imaging, and pathology. *Alzheimer's Research & Therapy*, *8*(1), 52. https://doi.org/10.1186/s13195-016-0219-5

Lee, D., & Newman, S. D. (2010). The effect of presentation paradigm on syntactic processing: An event-related fMRI study. *Human Brain Mapping*, *31*(1), 65–79. https://doi.org/10.1002/hbm.20845

Matchin, W., Basilakos, A., Ouden, D.-B. D., Stark, B. C., Hickok, G., & Fridriksson, J. (2022). Functional differentiation in the language network revealed by lesion-symptom mapping. *NeuroImage*, *247*, 118778. https://doi.org/10.1016/j.neuroimage.2021.118778

Matchin, W., den Ouden, D.-B., Basilakos, A., Stark, B. C., Fridriksson, J., & Hickok, G. (2023). Grammatical parallelism in aphasia: A lesion-symptom mapping study. *Neurobiology of Language*, *4*(4), 550–574. https://doi.org/10.1162/nol_a_00117

Matchin, W., Mollasaraei, Z. K., Bonilha, L., Rorden, C., Hickok, G., den Ouden, D., & Fridriksson, J. (2024). Verbal working memory and syntactic comprehension segregate into the dorsal and ventral streams, respectively. *Brain Communications*, *6*(6), fcae449. https://doi.org/10.1093/braincomms/fcae449

Mayer, A. R., Ryman, S. G., Hanlon, F. M., Dodd, A. B., & Ling, J. M. (2017). Look hear! The prefrontal cortex is stratified by modality of sensory input during multisensory cognitive control. *Cerebral Cortex*, *27*(5), 2831–2840. https://doi.org/10.1093/cercor/bhw131

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Group, T. P. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine*, *6*(7), e1000097. https://doi.org/10.1371/journal.pmed.1000097

Müller, V. I., Cieslik, E. C., Laird, A. R., Fox, P. T., Radua, J., Mataix-Cols, D., Tench, C. R., Yarkoni, T., Nichols, T. E., Turkeltaub, P. E., Wager, T. D., & Eickhoff, S. B. (2018). Ten simple rules for neuroimaging meta-analysis. *Neuroscience & Biobehavioral Reviews*, *84*, 151–161. https://doi.org/10.1016/j.neubiorev.2017.11.012

Noonan, K. A., Jefferies, E., Visser, M., & Lambon Ralph, M. A. (2013). Going beyond inferior prefrontal involvement in semantic control: Evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *Journal of Cognitive Neuroscience*, *25*(11), 1824–1850. https://doi.org/10.1162/jocn_a_00442

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. *Journal of Neuroscience*, *37*(36), 8755–8766. https://doi.org/10.1523/JNEUROSCI.0660-17.2017

Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., … Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *BMJ*, *372*, n71. https://doi.org/10.1136/bmj.n71

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*(12), 976–987. https://doi.org/10.1038/nrn2277

Poletiek, F. H., Monaghan, P., van de Velde, M., & Bocanegra, B. R. (2021). The semantics-syntax interface: Learning grammatical categories and hierarchical syntactic structure through semantics. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *47*(7), 1141–1155. https://doi.org/10.1037/xlm0001044

Pylkkänen, L. (2019). The neural basis of combinatory syntax and semantics. *Science*, *366*(6461), 62–66. https://doi.org/10.1126/science.aax0050

Rochon, E., Kave, G., Cupit, J., Jokel, R., & Winocur, G. (2004). Sentence comprehension in semantic dementia: A longitudinal case study. *Cognitive Neuropsychology*, *21*(2), 317–330. https://doi.org/10.1080/02643290342000357

Rodd, J. M., Vitello, S., Woollams, A. M., & Adank, P. (2015). Localising semantic and syntactic processing in spoken and written language comprehension: An Activation Likelihood Estimation meta-analysis. *Brain and Language*, *141*, 89–102. https://doi.org/10.1016/j.bandl.2014.11.012

Saffran, J. R. (2020). Statistical language learning in infancy. *Child Development Perspectives*, *14*(1), 49–54. https://doi.org/10.1111/cdep.12355

Satpute, A. B., Badre, D., & Ochsner, K. N. (2014). Distinct regions of prefrontal cortex are associated with the controlled retrieval and selection of social information, *Cerebral Cortex*, *24*(5), 1269–1277. https://doi.org/10.1093/cercor/bhs408

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. https://doi.org/10.1016/j.cortex.2017.09.002

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proceedings of the National Academy of Sciences*, *106*(1), 322–327. https://doi.org/10.1073/pnas.0805874106

Siegelman, M., Blank, I. A., Mineroff, Z., & Fedorenko, E. (2019). An attempt to conceptually replicate the dissociation between syntax and semantics during sentence comprehension. *Neuroscience*, *413*, 219–229. https://doi.org/10.1016/j.neuroscience.2019.06.003

Sitnikova, T., Rosen, B. R., Lord, L.-D., & West, W. C. (2014). Understanding human original actions directed at real-world goals: The role of the lateral prefrontal cortex.

NeuroImage, *103*, 91–105. https://doi.org/10.1016/j.neuroimage.2014.09.012

Stampacchia, S., Pegg, S., Hallam, G., Smallwood, J., Lambon Ralph, M. A., Thompson, H., & Jefferies, E. (2019). Control the source: Source memory for semantic, spatial and self-related items in patients with LIFG lesions. *Cortex*, *119*, 165–183. https://doi.org/10.1016/j.cortex.2019.04.014

Stampacchia, S., Thompson, H. E., Ball, E., Nathaniel, U., Hallam, G., Smallwood, J., Lambon Ralph, M. A., & Jefferies, E. (2018). Shared processes resolve competition within and between episodic and semantic memory: Evidence from patients with LIFG lesions. *Cortex*, *108*, 127–143. https://doi.org/10.1016/j.cortex.2018.07.007

Thompson, H. E., Almaghyuli, A., Noonan, K. A., Barak, O., Lambon Ralph, M. A., & Jefferies, E. (2018). The contribution of executive control to semantic cognition: Convergent evidence from semantic aphasia and executive dysfunction. *Journal of Neuropsychology*, *12*(2), 312–340. https://doi.org/10.1111/jnp.12142

Thompson, H. E., & Jefferies, E. (2013). Semantic control and modality: An input processing deficit in aphasia leading to deregulated semantic cognition in a single modality. *Neuropsychologia*, *51*(10), 1998–2015. https://doi.org/10.1016/j.neuropsychologia.2013.06.030

Thompson, H. E., Noonan, K. A., Halai, A. D., Hoffman, P., Stampacchia, S., Hallam, G., Rice, G. E., De Dios Perez, B., Lambon Ralph, M. A., & Jefferies, E. (2022). Damage to temporoparietal cortex is sufficient for impaired semantic control. *Cortex*, *156*, 71–85. https://doi.org/10.1016/j.cortex.2022.05.022

Thompson, S. P., & and Newport, E. L. (2007). Statistical learning of syntax: The role of transitional probability. *Language Learning and Development*, *3*(1), 1–42. https://doi.org/10.1080/15475440709336999

Tobyne, S. M., Osher, D. E., Michalka, S. W., & Somers, D. C. (2017). Sensory-biased attention networks in human lateral frontal cortex revealed by intrinsic functional connectivity. *NeuroImage*, *162*, 362–372. https://doi.org/10.1016/j.neuroimage.2017.08.020

Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012). Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Human Brain Mapping*, *33*(1), 1–13. https://doi.org/10.1002/hbm.21186

Turker, S., Kuhnke, P., Eickhoff, S. B., Caspers, S., & Hartwigsen, G. (2023). Cortical, subcortical, and cerebellar contributions to language processing: A meta-analytic review of 403 neuroimaging experiments. *Psychological Bulletin*, *149*(11–12), 699–723. https://doi.org/10.1037/bul0000403

Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., Papoutsi, M., & Stamatakis, E. A. (2011). Left inferior frontal cortex and syntax: Function, structure and behaviour in patients with left hemisphere damage. *Brain*, *134*(2), 415–431. https://doi.org/10.1093/brain/awq369

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, *30*(4), 1414–1432. https://doi.org/10.1016/j.neuroimage.2005.11.002

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., Mellet, E., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? *NeuroImage*, *54*(1), 577–593. https://doi.org/10.1016/j.neuroimage.2010.07.036

Wang, X., Bernhardt, B. C., Karapanagiotidis, T., De Caso, I., Gonzalez Alam, T. R. del J., Cotter, Z., Smallwood, J., & Jefferies, E. (2018). The structural basis of semantic control: Evidence from individual differences in cortical thickness. *NeuroImage*, *181*, 480–489. https://doi.org/10.1016/j.neuroimage.2018.07.044

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011). The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cerebral Cortex*, *21*(5), 1066–1075. https://doi.org/10.1093/cercor/bhq180

Zaccarella, E., Schell, M., & Friederici, A. D. (2017). Reviewing the functional basis of the syntactic Merge mechanism for language: A coordinate-based activation likelihood estimation meta-analysis. *Neuroscience & Biobehavioral Reviews*, *80*, 646–656. https://doi.org/10.1016/j.neubiorev.2017.06.011