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Title: Localising semantic and syntactic processing in spoken and written language comprehension: An Activation Likelihood Estimation meta-analysis

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Abstract: We conducted an Activation Likelihood Estimation (ALE) meta-analysis to identify brain regions that are recruited by linguistic stimuli requiring relatively demanding semantic or syntactic processing. We included 54 functional MRI studies that explicitly varied the semantic or syntactic processing load, while holding constant demands on earlier stages of processing. We included studies that introduced a syntactic/semantic ambiguity or anomaly, used a priming manipulation that specifically reduced the load on semantic/syntactic processing, or varied the level of syntactic complexity. The results confirmed the critical role of the posterior left inferior frontal gyrus (LIFG) in semantic and syntactic processing. These results challenge models of sentence comprehension highlighting the role of anterior LIFG for semantic processing. In addition, the results emphasise the posterior (but not anterior) temporal lobe for both semantic and syntactic processing.

Our results confirm the critical role of left inferior frontal gyrus (LIFG) in semantic and syntactic processing, but provide partial support for an anterior-posterior dissociation in semantic-syntactic processing in LIFG. A second key finding was the clear emphasis on posterior (and not anterior) temporal lobe for semantic and syntactic processing.

Highlights

- The neural bases of semantic and syntactic aspects of comprehension were examined
- An Activation Likelihood Estimation (ALE) Meta-analysis was conducted
- Results confirm a role of posterior LIFG in both semantic and syntactic processing
- There was a clear emphasis on the posterior (and not anterior) temporal lobe

Reviewer #2

“1. There are several issues with study selection. Most critically, all of the syntactic studies involve sentences (by definition, I guess), whereas a large subset of the semantic studies are single word studies. This means that the syntax/semantics comparison is confounded by this significant difference in the presence/absence of combinatorial structure. The authors mention this limitation in the discussion, but I was not fully satisfied. Is it really not possible to do an analysis with only the sentence-level or higher studies?”

We agree that this is an important and unfortunate difference in approach between the two fields. We attempted to address this by running an additional analysis without the following studies, which used words, word pair, or fragments: Bedny et al. 2008, Bonhage et al. in press, Copland et al., 2003, Giesbrecht et al., 2004, Wheatley et al., 2005, Grinrod et al., 2008, Whitney et al., 2009, Chan et al., 2004, Han et al., 2007, Hargreaves et al., 2011, Kotz et al, 2002, Rissmann et al., 2003, Ruff et al., 2008, Herrmann et al., 2012, Brennan et al.*, 2012, Segaert et al., 2012*, Segaert et al., 2013* (*requested to be removed from the analysis by reviewer in comment 2). However, note that upon running the contrast analysis, GingerALE issued a warning stating that: “The contrast analysis is unlikely to have enough statistical power to show a significant difference with less than about fifteen experiments in each data set.” We therefore prefer not to include the results of the analysis on only the studies using sentences as stimuli in the paper.

The current version of the Discussion includes the following:

“Any difference found between semantic and syntactic studies may have been affected by the fact that all syntactic studies except for one (Herrmann, Obleser, Karlerlah, Haynes, & Friederici, 2012) who used two-word utterances) used sentences or narratives, while four of the semantic studies used single words, eight used word pairs or word triplets, and 14 used sentences (Table I). We were not able address this confound, e.g., by examining differences between semantic and syntactic studies without inclusion of the studies using word stimuli, as this would result in comparing a group of 27 experiments with one with 14 experiments, which is not advisable as the power would be too low for the subtraction analysis in GingerALE. ” (p25)

2. Personally I do not think that "anomaly" studies have much value, so I would not have included them. We don't have any theories of what anomaly processing involves, and I think

it is far from obvious that syntactic anomalies would lead to increased signal in syntactic processing regions, and semantic anomalies would lead to increased signal in semantic processing regions, and that is basically what is being assumed. It has never been demonstrated, and it just isn't a safe assumption.

We entirely share the reviewer's reservations about the value of anomaly studies (see Davis & Rodd, 2011 for discussion of this precise issue). However, this approach is widely used within the field, indicating that our reservations are not widely held and we were concerned that omitting these studies could be perceived as a form of selection bias. To address this concern, we have now added an analysis that excludes the following ten studies that use an anomaly manipulation: Baumgaertner et al. 2002, Friederici et al. 2006, Friederici et al. 2010, Herrmann et al. 2012, Kambara et al. 2013 (semantic contrast), Kambara et al. 2013 (syntactic contrast), Kiehl et al. 2002, Kuperberg et al. 2000, Nieuwland et al. 2012 (semantic contrast), and Tesink et al. 2009. This left 45 experiments (Table V).

"I would also exclude the Brennan study since it is just as much semantic as syntactic, and the Segaert studies since it's unclear that syntactic priming modulates syntactic load." Brennan et al., 2012, Segaert et al., 2012, Segaert et al., 2013 have been excluded from the analysis.

"3. The description of the keywords used is vague, e.g. "appropriate combinations of these keywords". Given that this is a formal meta-analysis, I think a precise description of the search should be provided."

The keywords mentioned in the paper: "speech", "reading", "auditory", "comprehension", "fMRI", "PET", "narrative", "sentence", "word", "neuroimaging", "priming", "repetition suppression", "ambiguity", "anomaly", "incongruent", "congruent", "syntactic", "complexity", "context" and appropriate combinations of these keywords, resulted in the retrieval of the majority (~90%) of the included papers. In addition, we collected the remaining 10% papers by searching for prominent researchers in the field in pubmed and by checking these researchers websites for papers in press.

"4. There are confusing aspects to the results. The results and table 4 describe a semantic cluster in the left STG, but it is not visible in the figure, despite having an x peak (-58) only 4 mm from the sagittal slice shown (-54). This seems like something is wrong. The syntax

analysis is said in the text to have resulted in a cluster in the right MTG, but in the figure I see something in the left STS, and the table shows left MTG. I am assuming the "right MTG" in the text is the mistake, but I can't be sure. All results, tables, and figures need to be carefully checked for correctness and consistency."

We have checked all results, tables, and figures in the current revision, after performing a re-analysis of all data.

"5. I don't mind that the discussion is arranged around three general brain areas, but I had a problem with the way it was framed in terms of the results from the contrast in Fig 1, which just lumped all the studies in together. It seems incorrect to claim that these regions are "consistently activated" (p. 18), because they could have just been activated in many studies of one type, and that might be enough to be significant in the whole meta-analysis. The only region which is actually shown to be consistently activated is the left IFG pars opercularis, since it is yellow in Fig 2A. I would reframe the discussion around Fig 2A and Fig 3A, since those are the interesting findings."

We agree that the use of the word "consistently" was too strong in this context and have removed it. However we feel that it is important to discuss all of the regions that are emphasised by the main analysis. Our view is that the individual contrasts between syntax and semantics help to refine our thinking about the function of the brain regions identified in the main analysis, and we would not want to preclude a region that emerged in the main analysis from discussion purely because it did not come up in any of the individual contrasts, which are necessarily less well powered than the main contrast.

6. I didn't really find the spoken/written analyses very interesting. They seem to distract from the main focus of the paper.

The spoken/written analysis has been removed from the paper in response to the reviewer's comment.

Other comments"

pp. 3-4. Suggest citing Wilson et al. (2014) (already included in meta-analysis) as one of the studies arguing for a posterior temporal rather than anterior temporal locus for syntactic processing, since it is probably the study that addresses this question most directly."

We added Wilson et al (2014) as suggested by the reviewer to p. 3-4.

p. 4. The phrase "clear dissociation" suggests that the authors are endorsing Dapretto & Bookheimer's findings. Given the poor task design of that study, I'd suggest simply "dissociation".

We removed the word "clear".

"p. 6. This sentence seemed weak: "However, there are no published meta-analyses that focus specifically on higher-level stages of language comprehension without including less specific contrasts such as word vs. nonwords." Which study are you trying to distinguish yourself from here? Vigneau? Please be more explicit. If this is the first study apart from Vigneau to meta-analyze syntax vs semantics, then just say that, and point out weaknesses of Vigneau (which shouldn't be hard to do)."

We agree that this was unclear and have now clarified the novel contribution of this paper making clear the key difference to the Vigneau meta-analysis.

"pp. 10-11. It would be sufficient just to say which version of GingerALE was used, rather than explaining why it's slightly better than the previous version."

We changed this as suggested by the reviewer in the revision on p. 11.

"p. 13. The long awkward sentence describing the different tasks used could just be replaced with a reference to the table which already provides this information."

We changed this as suggested by the reviewer on p. 13.

"p. 14. I wonder if Tyler et al. (2004) "Processing Objects at Different Levels of Specificity" JOCN would qualify as a study manipulating semantic complexity?"

We excluded this study from the analysis, as it uses picture stimuli. The current study is confined to studies of spoken and written language.

"p. 18. To my knowledge the earliest claim for a posterior/anterior syntax/semantics distinction comes from Dapretto & Bookheimer, 1999; this should be cited here."

We now cite Dapretto & Bookheimer (1999) as suggested.

"p. 19. Why is the Badre account discussed, when you have no semantic findings in the pars orbitalis?"

We feel it is important to mention this account in the introduction as it sets up the prediction that semantic processing might be associated with primarily anterior aspects of the LIFG. Similarly in the discussion it is relevant to our argument that anterior LIFG activation may be restricted to explicit semantic decision tasks, and not to the forms of semantic comprehension being addressed in the current study.

“p. 22. Again cite Wilson 2014 for posterior vs anterior syntax.”

We added Wilson et al (2014) as suggested.

“p. 23. Mummy et al. (1999) Brain seems very relevant to the posterior ITG cluster for semantics.”

We added this paper as suggested.

“p. 24. I disagree that there are any signal issues with anterior STG. I have never seen dropout in that region.”

The Devlin et al., paper cited does include anterior STG as a region where more activation is seen in a PET study than in a comparable fMRI study, indicating that signal dropout is an issue, albeit to a lesser extent than more inferior portions of the temporal lobe. We have modified our comment to acknowledge that signal dropout is likely to be less severe in this region.

“pp. 26-27. Why are you concerned that regions recruited for both syntax and semantics are missed, when you have Fig 1 which should reveal regions recruited for both?”

We have clarified this comment, to be clear that we were referring to brain regions that might have been equally recruited to the low- and high-demand conditions in the contrasts included in this analysis.

In addition, all the minor comments have been addressed in the revision.

Reviewer #3

-Some additional detail on the selection of studies for inclusion would be helpful. I.e., how many studies were identified through a pubmed search, and how many were added to this by the authors? How many were excluded for various reasons? The authors inclusion criteria seem reasonable but it would give the reader additional confidence to better understand how they were applied. Off the top of my head there seem to be some papers missing from the labs of David Caplan, Angela Friederici , Murray Grossman, Marcel Just, and some other researchers who have spent some time doing syntax. It could well be these failed to meet the inclusion criteria and I don't expect a list of every article considered, but more detail would help me to feel assured in the final set of articles that were selected.”

See our response to reviewer #2 on this issue. Note that studies referred to by the reviewer were considered for inclusion, but were excluded, as they did not fit our criteria. For instance, Friederici et al. (2000), Just et al (1996) and Caplan et al. (1999) all used ROI analyses was excluded as this was a ROI analysis and did not include the necessary results tables.

“-The introduction could perhaps be helpfully reframed a bit. On p. 3 the authors note a "high level agreement about which brain regions are important" and that the disagreement is more about the functional roles. However, the discussion about, for example, subdivisions of the IFG for semantic/syntactic processing seems more concerned with "where" (similarly with posterior vs. anterior temporal cortex). I think that selection (or conflict resolution) processes in the IFG are appealing as a unifying theme in the discussion; however, I think this could have been better set up in the introduction as well.”

We agree that this section of the introduction was poorly phrased, and have modified the introduction to remove the statement that the “where” question has been resolved. We have also introduce the important conflict resolution account, albeit briefly as this is dealt with more comprehensively in the Discussion.

“-With respect to localization, another important consideration must surely be the spatial spread that comes from averaging over studies (which average over individuals). I realize there is no way around that in the current meta-analysis, but it would be important to acknowledge this in the discussion. Finding overlap between ALE clusters for syntax and semantics suggests a shared system, but I don't think it's particularly strong evidence, given the cytoarchitectonic and functional variability observed in this regions.”

We now include a section on this important issue in the ‘limitations’ section of the discussion.

“-p. 6 and elsewhere - it's fine to focus on semantic processing in a linguistic sense; to my mind this complements the Binder et al. (2009) meta analysis, which I would characterize as more focused on semantic representation. Currently some of the attempts to distinguish the current work from the Binder et al. meta analysis were more distracting than helpful. It may help clarify to focus on levels of difficulty, as opposed to the most basic construct.”

We have removed this comparison to the Binder et al meta-analysis, which we agree was unhelpful. We gave considerable thought to the possibility of adding further discussion on the issue of ‘basic’ semantic representation vs. higher level semantic processing, but concluded that that the current meta-analysis cannot distinguish between these two aspects, and it would therefore be confusing to emphasize this distinction to the reader. We therefore decided to mention this only briefly at the end of the paper where we discuss future directions for this area of research.

“-A similar issue exists with syntax, for example, with respect to anterior temporal cortex. In the current report the authors have excluded sentences > word lists, for understandable reasons. However, it is also reasonable to think that there are levels of syntax (or "unification") that might show up in sentences > word lists, but not in object relative vs. subject relative sentences, or whatever higher level difficulty manipulation was chosen for inclusion. Thus, for both semantic and syntactic processing, the manuscript would benefit greatly from a bit more careful wording about which processes are being reflected (and how these results are characterized). This would help support the strong but interesting claim that both processes relied on a shared selection-supporting resource in left IFG.”

We agree that this approach may well miss out some of the more ‘basic’ processes that are activated by all the conditions in the relatively high level contrasts we selected. This issue was mentioned in the earlier version in the ‘limitations’ section of the discussion, but has been rewritten to make the issue clearer (see response to Reviewer 2).

“Minor comments:

-p. 11 what does pID stand for?”

pID is short for p-value threshold with assumptions of independence. The False Discovery Rate (FDR) finds a threshold for p-values that are either probabilistically independent or non-parametrically related (p InDpendent and p Nonparametric, or pID and pN in GingerALE).

“-p. 12 FDR $q < .001$ (or $< .05$) is appropriate, as is the Monte Carlo approach. I am less convinced by the cluster extent threshold. This seems arbitrary in the first place, and particularly arbitrary to move up to 400 from 200 mm³. Although we obviously don't want to over interpret results, the FDR correction is principled, whereas the cluster extent is not. I'd like to see the full results at least in tables, even if not displayed (but is there any reason not to display them?).”

We chose the more stringent 400mm³ threshold as this was chosen also for the two meta-analyses described in Adank (2012a, 2012b). But in response to this comment we now report the more comprehensive set of results that reach this more conventional threshold.

“-p. 15 For the main comprehension network, all 56 studies were included. However, 26 were for semantic studies, and 30 for syntax. Including all without differentially weighting would result in a slight bias for syntax (more studies) than semantics, would it not? Is it possible to weight these so that semantics and syntax contribute equally to the final result? (I.e. in a traditional SPM group analysis, one could model an independent samples t-test, with a [.5 .5] contrast).”

Unfortunately, it is not possible to add a weighting in GingerALE for unbalanced groups. In addition, the updated analysis has smaller group differences, as group sizes for semantic and syntactic studies are now 26 and 28, respectively.

“-p. 23-24 The damage in semantic dementia can be quite variable, and the region that contributes most heavily to their impairment is still a matter of debate. Thus, I think the summary here is too short to do the issue justice, and I would suggest taking it out.”

We removed this section from the paper.

Localising semantic and syntactic processing in spoken and written language
comprehension: An Activation Likelihood Estimation meta-analysis

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Abstract

We conducted an Activation Likelihood Estimation (ALE) meta-analysis to identify brain regions that are recruited by linguistic stimuli requiring relatively demanding semantic or syntactic processing. We included 54 functional MRI studies that explicitly varied the semantic or syntactic processing load, while holding constant demands on earlier stages of processing. We included studies that introduced a syntactic/semantic ambiguity or anomaly, used a priming manipulation that specifically reduced the load on semantic/syntactic processing, or varied the level of syntactic complexity. The results confirmed the critical role of the *posterior* left inferior frontal gyrus (LIFG) in semantic *and* syntactic processing. These results challenge models of sentence comprehension highlighting the role of *anterior* LIFG for semantic processing. In addition, the results emphasise the posterior (but not anterior) temporal lobe for both semantic and syntactic processing.

Key words: Syntax, Semantics, Neuroimaging, Meta-analysis, Methodology, fMRI

1. Introduction

The task of understanding the meaning of a sentence has many component parts. Readers and listeners must retrieve the meaning of each individual word and they must also combine words according to the sentence's syntactic structure to determine how the words relate to each other (e.g., "the boy kissed the girl" vs. "the girl kissed the boy"). In addition, they must use each word's meaning to constrain the precise interpretation of other words in the sentence (e.g., the meaning of the word "bark" in "the bark of the dog" versus "the bark of the tree"). A large number of neuroimaging studies have implicated, with a relatively high level of consistency, several core brain regions as being important for these semantic and syntactic aspects of sentence comprehension (Friederici, 2012; Price, 2012). These regions include, but are not restricted to, left Inferior Frontal Gyrus (LIFG) and anterior and posterior temporal regions.

However, despite the relatively large number of published papers on this topic the field has not yet reached a consensus on several key issues. For instance, Friederici (2012) has outlined a model of spoken language comprehension that emphasizes the role of a ventral pathway that emerges anteriorly from Heschl's Gyrus in constructing the meaning of sentences. Here, sound-to-meaning mapping is localised in the portion of the Superior Temporal Gyrus (STG) that is anterior to Heschl's Gyrus, while a more anterior region of the superior temporal cortex performs general combinatorial processes involved in processing syntactic phrase structure and in combining word meanings. In contrast, others have emphasized the role of the *posterior* portion of the inferior or middle temporal gyri for the function of accessing word meanings on the basis of their spoken form (Hickok & Poeppel, 2007; Poeppel, Emmory, Hickok, & Pylkkanen, 2012; Rodd, Johnsrude, & Davis, 2012) and for

syntactic processing of sentences (e.g., Griffiths, Marslen-Wilson, Stamatakis, & Tyler, 2013; Tyler et al., 2011; 2014).

Disagreement also exists regarding the functional organization of LIFG. Friederici (2012) argues for a strict dissociation on the basis of the linguistic nature of the information to be processed, namely that the frontal operculum and pars opercularis (BA44) sub serve syntactic processing, while the more anterior regions of pars triangularis and pars orbitalis (BA 45 and 47) support semantic processing. Others have suggested a more graded distinction along these lines, such that semantic processing is primarily associated with a more anterior portion of the LIFG compared with syntactic processing, but with substantial overlap in function reflecting the interactive nature of the underlying cognitive processes (Hagoort, 2005). Under this view, the most posterior portion of the LIFG is primarily associated with phonological aspects of comprehension (Gold, Balota, Kirchhoff, & Buckner, 2005; Gough, Nobre, & Devlin, 2005). In contrast, other authors have argued that there is *no* clear dissociation between semantic and syntactic processing within frontal cortex (Rodd, Longe, Randall, & Tyler, 2010) or that activation of this region varies primarily as a function of task demands (Wright, Randall, Marslen-Wilson, & Tyler, 2011). Similarly, the influential conflict resolution account (Novick, Kan, Trueswell, & Thompson-Schill, 2009; Novick, Trueswell, & Thompson-Schill, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) of LIFG function, proposes that posterior LIFG (BA44/45) plays a general role in resolving competition between multiple activated representations for syntactic as well as semantic aspects of comprehension (Novick et al., 2005).

This lack of consensus is firstly due to inconsistencies in published results that may be due to heterogeneity in experimental design across studies. For example,

Dapretto and Bookheimer (1999) report a dissociation between the recruitment of anterior LIFG for semantic processing and posterior LIFG for syntactic processing, while Rodd et al. (2010) report that semantic *and* syntactic manipulations activated the same region of posterior LIFG. When combined with activation of this area during phonological processing (e.g., Rumsey et al., 1997), this latter finding implicates the posterior LIFG (at least) as a multifunctional region. This inconsistency is hard to interpret because these two studies that contrast semantic and syntactic processing differ both in terms of multiple important properties of the stimuli used (visual vs. auditory; words vs. sentences), and also in the tasks used (semantic judgment tasks vs. sentence comprehension). This heterogeneity is typical of the field and illustrates a recurrent problem facing researchers when they try to evaluate the likely cause of discrepancies between individual studies, and the extent to which some findings might result from the limitations of particular experimental paradigms. For example, some researchers (Davis & Rodd, 2011) have raised concerns about the reliance of the field on paradigms that study semantic or syntactic processing by introducing a semantic or syntactic anomaly (e.g., Friederici & Kotz, 2003; Kuperberg et al., 2000). These studies typically assume that by disrupting one specific linguistic property of a sentence it is possible to isolate the brain regions involved in that aspect of processing. In contrast to the ERP paradigms that have used this ‘anomaly’ approach with great success to reveal the time course of sentence processing, fMRI paradigms rely on a slow haemodynamic response that smears together in time participants’ initial response to an anomaly with subsequent processes that are triggered by their detection of the anomaly. For example, when participants encounter a syntactic anomaly, they may engage in additional semantic processes as they try and make sense of what they have read/heard. Alternatively, they may respond to some

anomalies by “giving up” and thus reducing the extent to which both semantic or syntactic information is processed (Kuperberg et al., 2000). Thus it is not clear whether this paradigm can successfully dissociate these two aspects of sentence processing, and whether findings will necessarily be replicated using alternative approaches.

A second reason for the lack of consensus in the field is that each individual study is usually (deliberately) restricted to look at responses to stimuli from a particular domain (auditory vs. visual) or that contain ambiguities or anomalies of a very particular type. Furthermore, given the combinatorial nature of syntax and the wide variety of syntactic constructions that are permitted in natural language, each experiment necessarily samples only a limited range of types of possible sentence structures from the vast possible range of linguistic constructions. This feature of experimental designs can make it difficult to determine the extent to which results should be generalised to other types of stimuli or to other linguistic operations.

We addressed these two limitations by integrating the results across multiple studies in a formal meta-analysis. This approach allowed us to determine which results are consistent across a range of experimental approaches, and which results are more likely to reflect idiosyncratic aspects of a particular study or experimental approach. We expected that this meta-analysis would enable us to identify which areas might be consistently engaged in semantic and syntactic processing across modality of input (auditory/visual) over a wide variety of experimental manipulations and behavioural tasks.

Several published meta-analyses address issues in language comprehension, for instance, focusing on processing at the level of single words (Turkeltaub, Eden, Jones, & Zeffiro, 2002), intelligibility processing at word and sentence level (Adank, 2012a),

semantic processing in general (Binder, Desai, Graves, & Conant, 2009), and the role of the left hemisphere in processing phonology, semantics, and sentence processing (Vigneau et al., 2006). However, there are no published meta-analyses that directly contrast semantic and syntactic processing. The Vigneau et al., (2006) analysis compares contrasts that are categorised as ‘semantic processing’ or ‘sentence processing’, but the latter set of contrasts include those that inevitably also load on semantic aspects of sentence processing (e.g., sentences vs. unlinked words; sentences with high vs. low mental imagery content). In addition, the Vigneau et al. analysis does not include the relatively large set of studies that have used semantic ambiguities/anomalies to investigate semantic processing at a sentence level. Therefore, we aimed to map out the neural network associated with how language users resolve two types of higher-level problems during language comprehension, namely computing the meanings of words (in isolation or in context) and the syntactic structures of sentences. Importantly, we only included studies that explicitly varied the processing demand on the semantic/syntactic aspects of the linguistic material being processed, for example by the introduction of a semantic/syntactic ambiguity, complexity or anomaly, or by including a priming or relatedness manipulation that specifically reduced the processing load on these aspects of comprehension. We restricted our analysis to studies that include contrasts of this type while holding constant (i) the processing demands on lower-level form based processes and (ii) the task being performed. While our primary interest is in how these semantic/syntactic processes operate at the level of the sentence, we did not restrict the analysis to studies that use sentence materials, but also included studies using single words (or word pairs or triplets) where the experimental contrasts are clearly semantic in nature (e.g., semantic priming).

We used the Activation Likelihood Estimation (ALE) method (Laird et al., 2005; Turkeltaub et al., 2002), an objective and quantitative technique for meta-analysis of coordinates from neuroimaging results. ALE can be used to determine the overlap between coordinates obtained from neuroimaging studies by modelling them as probability distributions centred at the reported coordinates. The meta-analysis applies ALE to coordinates collected from neuroimaging studies investigating semantic or syntactic processing (or both).

ALE was first used to identify the network of brain regions that are consistently activated by these semantic/syntactic aspects of language comprehension. We anticipate that this analysis will reveal areas commonly identified in studies on semantic and syntactic processing, but may also reveal additional regions that may not previously have been the focus of extensive discussion. Second, we determined how activation in this network is modulated the linguistic nature of the experimental contrast (syntax vs. semantics).

The key contrast between studies that include semantic and syntactic manipulations could produce a range of different outcomes. Friederici (2012) emphasizes the differences between the networks of brain regions thought to be involved in these two key aspects of sentence comprehension: syntactic processing is most strongly associated with superior anterior temporal cortex, the frontal operculum, pars opercularis and the posterior portion of pars triangularis, while sentential semantic processing is associated with the more anterior portion of pars triangularis and pars orbitalis. This account therefore predicts that the contrast between these two types of linguistic manipulations should produce clear dissociations within these regions. In contrast, other authors have emphasized the commonalities in the regions that are activated by these two aspects of sentence

comprehension and suggest that differences in the nature of the task demands may be the key factor in producing variation in patterns of LIFG responses (Rodd et al., 2012; Rodd et al., 2010; Wright et al., 2011).

In summary, the aim of this meta-analysis was to first identify the set of brain regions that are involved in semantic or syntactic aspects of comprehension, by contrasting responses to stimuli that place specific increases on these aspects of comprehension with simpler linguistic stimuli.

2. Method

2.1. Selection of literature studies

We selected neuroimaging studies investigating language comprehension at post-lexical levels using Pubmed. We searched the Pubmed online database for studies using the keywords: “speech”, “reading”, “auditory”, “comprehension”, “fMRI”, “PET”, “narrative”, “sentence”, “word”, “neuroimaging”, “priming”, “repetition suppression”, “ambiguity”, “anomaly”, “incongruent”, “congruent”, “syntactic”, “complexity”, “context” and appropriate combinations of these keywords. In addition, we collected additional papers by searching for prominent researchers in the field.

2.2. Inclusion and exclusion criteria

Papers were included that fulfilled the following criteria: (i) neural responses were collected using fMRI or PET, (ii) only healthy, neurotypical subjects with intact hearing and no known neurological or psychiatric disorders were tested, (iii) the experiments contained conditions that explicitly manipulated the processing load on syntactic or semantic processing in spoken or written modalities, (iv) the paper included a table with foci for a comparison between conditions in which participants were processing stimuli that were more demanding to process versus those that were

less demanding to process, where the ‘demanding’ manipulation was either semantic or syntactic in nature, (v) the stimuli consisted of words or word pairs, word triplets, sentences, stories, or narratives; and (vi) results were reported at a group-level in a stereotactic 3-coordinate system. The following criteria were used to exclude papers from the analysis: (i) single subject studies, and (ii) studies that report only results from a pre-specified region-of-interest (ROI) analysis, or (iii) studies that contrasted meaningful stimuli with meaningless stimuli (e.g., words vs. pseudo-words), (iv) studies where the two critical conditions differed in the processing load on pre-semantic lexical access processes (e.g., primed vs. un-primed words in a single modality, i.e., repetition priming), (v) studies where the contrasts were likely to result in substantial differences in *both* semantic and syntactic processing (e.g., sentences vs. word lists, and sentences vs. ‘jabberwocky’ sentences for which both syntactic and combinatorial semantics are disrupted).

2.3. ALE methods

The ALE analysis was implemented using GingerALE 2.3 (www.brainmap.org), using the algorithm proposed in Turkeltaub et al. (2012). Coordinates collected from studies reporting coordinates in Talairach space were converted to MNI space using the `tal2icbm_spm` algorithm implemented in the GingerALE software (www.brainmap.org/ale).

GingerALE first computes modelled activation maps for each set of foci per included study. These foci are modelled as Gaussian distributions and merged into a single 3-dimensional volume. GingerALE uses an uncertainty modelling algorithm to empirically estimate the between-subjects and between-templates variability of all included foci sets. Second, ALE values are computed on a voxel-to-voxel basis by taking the values that are common to the individual modelled activation maps.

GingerALE constrains the limits of this analysis to a grey matter mask that was used to define the outer limits of MNI coordinate space, which excludes most white-matter structures (Eickhoff, Heim, Zilles, & Amunts, 2009). Furthermore, GingerALE does not take into account spatial smoothing kernels from individual papers, but determines spatial smoothing based on the number of participants in each experiment. Therefore, the number of participants was verified in each paper and participant numbers in Table I represent participants included in the neuroimaging analysis of each paper only (some studies excluded participants due to motion artefacts or technical difficulties).

We first ran a series of ALE analyses on (i) the complete set of studies and (ii) the two critical subsets of studies (syntactic, semantic) to explore the network of areas associated with each set and to examine the overlap between networks. These single studies were corrected for multiple comparisons using the FDR (false discovery rate) pID method at $q < 0.001$, voxel wise (default setting $q < 0.05$), using a cluster extent of 200mm^3 (default), following (Adank, 2012a, 2012b).

Second, we performed analyses that directly contrasted the ALE maps constructed above for the two key factors: linguistic type (semantic vs. syntactic). The first step consisted of running a series of two ALE analyses for (i) semantic contrasts, (ii) syntactic contrasts. These analyses were corrected for multiple comparisons using the FDR pID method at $q < 0.05$, voxel wise (default setting), using a cluster extent of 200mm^3 . In a second step, we used the thresholded ALE maps from the first step to run a series of subtraction analyses. These subtraction analyses were conducted using a FDR pID method at $q < 0.05$, voxel wise, again using a cluster extent of 200mm^3 , while the null distributions of the ALE scores were based on Monte Carlo simulations with 10,000 iterations. The ALE statistical maps for each subtraction analysis were

converted to voxel-wise probability maps based on these null distributions. The Mango software package (<http://ric.uthscsa.edu/mango/>) was used to view the resulting activation maps and all results were overlaid on a single MNI template available in Mango (Colin27_T1_seg_MNI.nii). We report only results for clusters that listed two or more experiments.

We used the Anatomy ToolBox for our anatomical localisation (Eickhoff, Heim, Zilles, & Amunts, 2006; Eickhoff et al., 2007; Eickhoff et al., 2005) in SPM8 (Wellcome Imaging Department, University College London, London, UK), as it provides localisation based on probabilistic maps included for several key areas of our study, including LIFG (Amunts et al., 1999), as expressed as a probability (in %) of a specific coordinate being located in Brodmann Areas (BA) 44 or 45.

--- *Insert Table I about here* ---

3. Results

3.1. Summary of included studies

We conducted the meta-analysis on studies that met the criteria for comprehension of semantic and syntactic processes. The studies in Table I were based on results from 54 fMRI experiments, 957 subjects, and 320 foci. No PET studies met the criteria. Stimuli were spoken or written single words, word pairs or triplets, sentence fragments, sentences, or narratives, and a variety of tasks were used. Finally, we also coded whether each experiment was conducted in a spoken or written modality, whether syntactic or semantic processing was examined, as well as the type of experimental manipulation used.

Experimental manipulations used across the studies were classified into six categories: ambiguity, anomaly, complexity, relatedness, cross-modal priming, and other. Although these classifications are not used in the analysis stage they provide an

important overview of the distribution of approaches used in the field, and in particular how these might differ across the categories of semantic and syntactic studies. Ambiguities were defined as stimuli for which multiple different semantic/syntactic representations were (temporarily) consistent with all or part of the linguistic input, but where it was possible for the listener/reader to resolve this ambiguity and produce a coherent, meaningful representation. Anomalies were defined as stimuli that contained an incongruous element that could not be integrated into the overall representation of the stimulus. A manipulation was classified as ‘complexity’ if the two contrasts differed in the complexity of the semantic/syntactic representation. In practice, this classification was only used for cases where the stimuli differed on the complexity of the resulting *syntactic* structure, as there were no equivalent studies of semantic complexity. A study was classified as ‘relatedness’ if it contrasted semantically related words/word pairs or sentences with semantically unrelated word pairs. Studies were classified as ‘cross-modal priming’ if they repeated semantic or syntactic stimuli in two different modalities, e.g., presenting a word/concept auditorily and as a picture. Some remaining studies did not fit into a single coherent category and were classified into a more general category of ‘other’, which included one experimental manipulation, namely establishing the contrast between sentences with high- or low-cloze probability. Table I shows the distribution of studies across the factors linguistic task (syntax vs. semantics) and stimulus presentation modality (reading vs. listening). Table I reveals a sharp difference in the main manipulations used by studies examining semantic or syntactic processing. The most striking difference is that 20 of the 28 syntax studies used a complexity manipulation (e.g., more versus less complex syntax), while no semantics studies

make use of this experimental manipulation. Instead, the included semantics studies use a wider variety of manipulations.

3.2. Main Comprehension Network

The main analysis included the data from all studies to identify regions that were more active for semantically/syntactically demanding stimuli. Figure 1 shows the main network of ALE clusters. Analysis of the experiments in Table I resulted in the ten significant clusters in Table II. The peaks of these clusters were distributed across left IFG (the central coordinates of the cluster were located in left POp and extended into Precentral Gyrus, PG, and PTr), left MTG extending into left STG, right IFG (POp and PTr), Precuneus, left IPL, left Inferior Temporal Gyrus (ITG), and left POrb (pars orbitalis).

--- Insert Table II and Figure 1 about here ---

3.3 Syntactic vs. Semantic Processing

We looked at the individual ALE clusters for (i) semantic and (ii) syntactic processing. The 54 studies were split into groups depending on whether they included a semantic contrast (26 studies, 167 foci) or a syntactic contrast (28 studies, 153 foci). Demanding semantic processing was associated with six ALE clusters (Table III and Figure 2), located in left pars opercularis (POp) of IFG, extending anteriorly into pars triangularis (PTr), left STG, left ITG, and left POrb. The analysis of studies addressing demanding syntactic processing resulted in eight ALE clusters, in Left POp (extending to PTr and left insula), Precuneus, left MTG, left PG, left SMA, left IPL, and left Supramarginal Gyrus (SMG).

--- Insert Table III and Figure 2 about here ---

Next, we directly compared the results from syntactic and semantic studies in a subtraction analysis using the procedure and significance levels outlined in section

2.3. GingerALE reported nine clusters for the contrast Semantics > Syntax, of which four contained the minimum of two or more contributing experiments (Table IV; Figure 3). The clusters were located in left ITG extending into Fusiform Gyrus (FFG), right Insula, and Left Superior Frontal Gyrus (SFG). GingerALE reported seven clusters for the contrast Syntax > Semantics, of which five contained two or more contributing experiments, located in left Superior Parietal Lobule (SPL) extending to Precuneus, left Middle Occipital Gyrus (MOG) extending into SPL and AG, left Superior Medial Gyrus (SMedG), left Insula extending into left POp, and left SMG extending into IPL.

--- Table IV and Figure 3 about here ---

Finally, we repeated the semantic vs. syntactic subtraction analyses with the omission of the 10 studies that used an anomaly manipulation (cf. Table I), which has been criticised by some authors for not strictly dissociating syntactic and semantic aspects of processing (Davis & Rodd, 2011). The remaining 44 studies (257 foci) were split into groups depending on whether they included a semantic (20 studies, 124 foci) or a syntactic contrast (24 studies, 133 foci). However, these exclusions did not result in an enhanced dissociation between the two forms of processing. The subtraction analysis showed five clusters for Semantics > Syntax, of which two listed two or more experiments. The first was located in left STG extending to MTG and the Rolandic Operculum and the second was located in left ITG extending into FFG (Table V, Figure 4). The subtraction analysis showed nine clusters for the contrast Syntax > Semantics, of which three contained two or more contributing experiments, located in left SPL extending to Precuneus, left POp in LIFG extending into the insula, and left PG.

--- Table V and Figure 4 about here ---

4. Discussion

The present study aimed to delineate the network of brain regions associated with processing semantic and syntactic aspects of language comprehension in a formal meta-analysis across 54 studies. The present meta-analysis differs from previous analyses (Adank, 2012a; Binder et al., 2009; Visser, Embleton, Jefferies, Parker, & Lambon-Ralph, 2010) in that we focused on how the linguistic system deals with comprehensible yet demanding linguistic stimuli and only included contrasts that specifically compared two types of meaningful stimuli that differed on the cognitive load placed on either semantic or syntactic aspects of comprehension. The initial analysis (Figure 1, Table II) highlighted a number of brain regions, discussed below, as being activated by these semantic or syntactic aspects of comprehension.

4.1. *Left Inferior Frontal Gyrus*

The largest cluster in the main analysis had its peak within pars opercularis, and extended anteriorly into pars triangularis, inferiorly into pars orbitalis and posteriorly and dorsally into the Precentral Gyrus (Figure 1; Table II). Subsequent analyses confirmed that both syntactic and semantic contrasts produced large (and partially overlapping) clusters within the posterior LIFG (Figure 2; Table III). In the case of syntax, the cluster is centred on pars opercularis and does not contain sub peaks within either pars triangularis or pars opercularis. In contrast, for semantics although the peak voxel is again within pars opercularis the cluster extends more dorsally than the syntactic cluster, and also includes a more anterior sub peak within pars triangularis as well as a separate small cluster in pars orbitalis.

This qualitative pattern seen in Figure 2 is confirmed, to some extent, by the direct subtraction contrast between syntax and semantics (Table IV; Figure 3), which

reveals a cluster with peaks in pars opercularis and the insula, confirming that this most posterior/ventral aspect of the main cluster is preferentially activated in studies of syntactic processing. This particular finding is (taken in isolation) consistent with the claim made by Friederici (2012), who argues that the frontal operculum and pars opercularis (BA44) subserve syntactic processing, and Hagoort (2005)'s claim that BA 44 and 45 make a particular contribution to syntactic processing. The reverse contrast, between semantic and syntactic processing is also somewhat compatible with these accounts: a corresponding 'semantic effect' is seen within both pars triangularis and pars orbitalis (Table IV), although it is important to emphasise that these effects only emerge when a relatively lenient statistical threshold is applied. However, although these isolated peaks can perhaps be taken evidence to support the anterior-posterior dissociation between semantic and syntactic aspects of processing there are two important caveats to this conclusion. First, the peak of the semantic-only cluster (Table III) lies within pars opercularis (i.e. in *posterior* LIFG), suggesting that although anterior LIFG may be additionally recruited by these studies of semantic processing compared with syntactic processing it appears that it is the more posterior region that is mostly strongly associated with *both* semantic and syntactic processing. This overlapping recruitment of posterior LIFG is most clearly shown in Figure 2. This strong association between posterior LIFG and semantic processing is inconsistent with those accounts that assert that such aspects of comprehension are primarily associated with anterior LIFG (Friederici, 2012; Hagoort, 2005). The finding that *both* semantic and syntactic aspects of comprehension are primarily associated with activation in the posterior LIFG is consistent with the influential conflict resolution account (Novick et al., 2009; Novick et al., 2005; Thompson-Schill et al., 1997) of LIFG function, which suggests that the posterior region of the LIFG

(BA44/45) plays a crucial role in resolving competition between activated representations to support the selection of a single representation. While this account has primarily been discussed with respect to *semantic* processing, these authors have explicitly noted the importance of these cognitive control processes for syntactic aspects of comprehension (Novick et al., 2005). In contrast to this proposed role for the *posterior* LIFG in conflict resolution, Badre and colleagues specifically attribute the *anterior* LIFG (pars orbitalis) to the controlled retrieval of semantic information from long-term memory (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2007). This process is required when stimulus-driven cues are insufficient to activate information relevant to one's goal or task, such as in the case of a semantic decision where two stimuli are weakly rather than strongly associated.

Our findings of posterior LIFG activation for both semantic and syntactic aspects of language comprehension can most easily be interpreted in this framework by assuming that resolving competition between activated representations is a core cognitive process that is routinely engaged when comprehending linguistic input that is relatively challenging to understand due to either its semantic or syntactic properties. For example in the case of a semantic/syntactic ambiguity it is clear that selection between multiple representations would be required, and it is at least plausible that the other manipulations such as the introduction of anomalies or syntactic complexities might result in more complex linguistic representations that necessitate increased demands on the processes that can select between the different pieces of information that are initially activated in response to each isolated word. In contrast, the limited extent of the anterior LIFG activation in the main contrast (Figure 1; Table II) and for the semantic condition alone (Figure 2) might indicate that 'controlled retrieval' plays a more limited role in the language comprehension

processes that are the focus of the studies included in this meta-analysis. Further studies are clearly needed to reveal the specific cognitive conditions that are required for anterior LIFG involvement in language comprehension.

An alternative account of the LIFG's role in language comprehension comes from Hagoort and colleagues (Hagoort, 2005, 2013; Hagoort, Baggio, & Willems, 2009). According to this theory, the LIFG constitutes a unification space that combines basic units of information to form larger complex representations of a sentence or discourse. In contrast to the conflict resolution account, this theory argues that it is combinatorial demands that drive activation in this region rather than conflict or selection load per se. According to this account, selection is merely one aspect of unification. This account is consistent with the findings of LIFG clusters found across a range of semantic and syntactic contrasts: all the ambiguity, anomaly, complexity and priming manipulations included in this meta-analysis would be predicted to directly increase the demands on these unification processes.

However, as previously discussed, the current data are not fully consistent with the unification account, which explicitly proposes functional specialisation across the LIFG such that semantic information is preferentially processed by pars orbitalis and pars triangularis, syntactic information by pars triangularis and pars opercularis and phonological processes by pars opercularis and premotor cortex. This fractionation is not consistent with our findings that semantic processing is primarily associated with *posterior* LIFG (pars opercularis/triangularis).

More generally, our results indicate that it may be premature to suggest that *any* region of the LIFG is specialised for semantic aspects of language comprehension. We suggest that the view that such an association exists has arisen primarily because of the focus in the semantic processing literature on explicit

semantic decision tasks and which load heavily on controlled retrieval of semantic information from long-term memory (e.g., Badre et al., 2005; Badre & Wagner, 2007; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Equivalent explicit judgement tasks are relatively rare in the syntactic processing literature. We suggest that the absence of extensive anterior LIFG clusters in this meta-analysis reflects our focus on studies that manipulate the difficulty of language *comprehension* processes, rather than comparing explicit semantic judgement tasks that vary on *task* difficulty. We suggest that to establish with any degree of certainty whether the function of the LIFG can be fractionated on the basis of the linguistic category of the information being processed requires additional studies which directly compare semantic and syntactic processing, while holding constant demands on processes such as selection, retrieval and working memory (see Rodd et al., 2010, for one attempt at such an approach).

Finally, it is important to consider the apparent lateralisation of this frontal activation. While the main analysis does reveal a right lateralised cluster of activation with sub peaks in both part opercularis and triangularis (Figure 1, Table II), this is very considerably reduced both in terms of extent and ALE value compared with its left hemisphere homologue, and it does not show a significant cluster in the separate analyses of semantic or syntactic processing or the direct contrast between them. The involvement of right hemisphere regions in comprehension is of particular theoretical interest given the relatively strong claims that have been made by some authors that it plays a critical role in maintaining non-selected word meanings in case subsequent reinterpretation is needed (e.g., Faust & Chiarello, 1998; Faust & Gernsbacher, 1996). The current approach, which is only able to reveal regions that are consistently recruited by a range of different semantic/syntactic computations,

does not provide a strong test of such very specific claims about the functional contribution of right hemisphere regions. All that can be concluded from these results is that there is evidence, albeit relatively weak, for the involvement of this region, and that future work is needed to determine the precise contribution of the right IFG.

4.2. *Left temporal lobe*

The second large cluster in the main analysis has its peak in posterior MTG, but extends superiorly (and anteriorly) into the mid STG (Figure 1; Table II). In contrast, there are no significant clusters in the more anterior regions of the superior temporal lobe that have been highlighted by some current accounts (e.g., Friederici, 2012) as being critical for sentential levels of processing for both semantic and syntactic information. Therefore these results seem more consistent with accounts that emphasize the role of the *posterior* portion of the inferior or middle temporal gyri in comprehension (Griffiths et al., 2013; Hickok & Poeppel, 2007; Mummery et al., 1999; Poeppel et al., 2012; Rodd et al., 2012; Tyler et al., 2011; Wilson et al., 2014).

The analyses that focus separately on semantic and syntactic processing help to clarify the roles of these different sub regions within the temporal lobe. The mid STG is only observed in the analysis of semantic processing, but is absent in the analysis of syntactic processing (Table III; Figure 2), and indeed shows more activation for semantic process albeit at a relatively low level of significance (Tables IV and V; Figure 3). This finding is somewhat surprising as this region is primarily associated with relatively low level auditory processing, rather than higher-level semantic aspects of processing. The sets of semantic and syntactic studies included here were relatively well balanced in terms of the proportion of studies that used auditory materials (semantics: 38% vs. syntax: 43%, see Table I) so it is unlikely that this finding reflects a simple selection bias. Given the wealth of evidence to support the

role of these per-auditory regions in speech *perception* not comprehension (Deschamps & Tremblay, 2014; Sætrevik & Specht, 2012; Turkeltaub & Coslett, 2010), we speculate that that this region is not actively engaged in the semantic processes of interest, but instead reflect a down-stream consequence of having attended to a ‘difficult’ stimulus, such as additional attentional resources being devoted to subsequent processing (cf., Binder et al., 2009, and Davis & Rodd, 2011, for further discussion). Further research is needed to determine what specific properties of hard-to-comprehend linguistic stimuli trigger the engagement of such regions and why, for this set of studies, this is preferentially occurring for the studies focusing on semantic processing.

In contrast to the semantic bias seen for STG, the posterior MTG region identified in the main analysis seems to be primarily associated with *syntactic* processing (Table III; Figure 2). This is consistent with theoretical accounts that attribute this region a key role in syntactic processing. (e.g., Griffiths et al., 2013; Tyler et al., 2011; Wilson et al., 2014). However it is important to note that although this region is seen only in the syntactic analysis and not the semantic analysis, it does not show a significant difference in its response to these two forms of processing (Tables III and IV; Figure 3), and so we remain cautious in attributing this region a role that is specific to syntactic processing. An alternative account of this region’s involvement in sentence comprehension, which is compatible with the current results, is that this region is only recruited for cases where the comprehended needs to reinterpret a part of a sentence that was initially misparsed (Rodd et al., 2012).

Finally, a third region of the left temporal lobe that emerges from these analyses as having a key role in comprehension is the left posterior ITG. Interestingly, this region is *only* significantly associated with semantic and not syntactic activation, and

the direct contrast between these two aspects of comprehension shows a large cluster of activation centred on the ITG but also including sub peaks within the fusiform gyrus. Parts of left fusiform gyrus have been associated with the representation of written word forms (e.g., Vinckier et al., 2007), but its implication here for both printed and spoken materials is consistent with studies showing activation in response to multiple inputs (Price & Devlin, 2003), concordant with a role for this region in integrating visual, semantic and phonological information (Price & Devlin, 2011). The association we observed between semantic processing and left fusiform gyrus activation also agrees with previous work showing a relationship between semantic errors in picture naming and integrity of BA 37 amongst acute stroke patients (Cloutman et al., 2009). However, the cluster we observed encompasses a large region of cortex and further work is needed to discover the functional roles of any adjacent regions.

It is notable that semantic processing was associated with activation in a relatively posterior part of the fusiform gyrus (BA 37), but no clusters were seen in the adjacent anterior fusiform gyrus (BA 20), which has been associated with multimodal semantic processing (Visser, Jefferies, & Lambon-Ralph, 2010). While posterior fusiform gyrus generates a clear MRI signal, the anterior inferior portions of the anterior temporal lobe are subject to considerable susceptibility artefact, and activation can also be missed when a restricted field of view is used (Visser, Embleton, et al., 2010). Although solutions to this problem have been recently developed (Visser & Lambon Ralph, 2011) many of the studies included here have not been designed to optimise signal in these regions, which renders the absence of its association with semantic processing in the current study difficult to interpret. It should also be noted that a similar issue arises when considering the absence of

activation in anterior superior temporal regions, as MRI signal in BA 38 is also vulnerable, albeit to a lesser extent, to susceptibility artefacts (Devlin et al., 2000). Future work considering the involvement of the anterior temporal regions in sentence level comprehension is therefore required.

4.3. Limitations

The conclusions drawn above need to be considered in the context of some general limitations of our methodological approach. Firstly, we must consider some general limitations of our meta-analysis that are shared by other recent meta-analyses (Luk, Green, Abutalebi, & Grady, 2011; Richlan, Kronbichler, & Wimmer, 2009; Turkeltaub & Coslett, 2010). First, these meta-analysis tools only allow us to consider the main effect of our key variable (i.e. syntax vs. semantics), but do not allow us either to look for interactions with other variables, or to partial out variance due to other potentially confounding variables. For example, the finding of a difference between syntactic and semantic processing in posterior LIFG should be treated with caution, for three reasons. First, we cannot be certain that a ‘syntactic’ cluster truly corresponds to the particular linguistic manipulation that was used in the syntactic studies included in our analysis, and not to some other processing demand that is more likely to be present in the majority of these syntactic studies, compared with the semantic studies. For example, we cannot rule out the possibility that the syntactic manipulations included in these experiments produce an enhanced load on verbal/phonological working memory processes compared with the semantic manipulations, particularly given the greater prevalence of sentence-level stimuli in the syntactic relative to semantic investigations. Any difference found between semantic and syntactic studies may have been affected by the fact that all syntactic studies except for one (Herrmann, Obleser, Karlerlah, Haynes, & Friederici, 2012)

who used two-word utterances) used sentences or sentence fragments, while four of the semantic studies used single words, eight used word pairs or word triplets, and 14 used sentences (Table I). We were not able to address this confound, e.g., by examining differences between semantic and syntactic studies without inclusion of the studies using word stimuli, as this would result in comparing a group of 27 experiments with one with 14 experiments, which is not advisable as the power would be too low for the subtraction analysis in GingerALE.

Likewise, when interpreting the observed overlap between the clusters produced by syntactic and semantic studies, it must be kept in mind that the meta-analysis process averages results over multiple studies, which have in turn averaged over individual participants. This approach can potentially lead to adjacent, but separate, clusters of activation, which may vary in precise location across individuals, appearing to overlap. Future studies are needed to determine whether additional functional specialization within the large clusters identified here can be observed within individual participants or in-group analyses with low levels of smoothing.

Perhaps more important than these general limitations of this approach are the issues that arise from our specific choices regarding which contrasts to include. In particular, our choice to only include contrasts between more demanding and less demanding stimuli conditions. This choice was made in order to assure that *all* of the regions we identified are recruited for semantic/syntactic aspects of comprehension and were not associated with lower-level phonological/lexical aspects of comprehension. This relatively selective approach may have had two separate and important consequences. First, it is possible that these analyses may be identifying regions that are not ‘core’ parts of the language processing network, but that are only recruited in response to specific unusual or idiosyncratic aspects of the more

demanding stimuli. Indeed a recent study of semantic ambiguity indicates that some of the posterior frontal and inferior temporal regions highlighted here are *not* routinely recruited by low-ambiguity sentences, having found that these kinds of sentences stimuli did not show increased activation compared with an unintelligible baseline (Vitello, Warren, Devlin, & Rodd, 2014) and some authors have suggested, for example, that portions of the LIFG are *only* recruited during sentence comprehension if the listener/reader is required to reinterpret a sentence (Novick et al., 2005; Rodd et al., 2012). An important point here is that, although these regions may not be automatically or obligatorily recruited for *all* sentences, that does not mean that they should not be considered core language comprehension regions. Natural language is replete with both semantic and syntactic ambiguities as well as syntactic complexity making it highly likely that the brain regions identified in this meta-analysis are necessary components of our comprehension system.

A related, but separate, issue is the possibility that this approach only highlights a subset of the brain regions involved in semantic and syntactic aspects of comprehension, specifically, that it may miss some core language processing regions involved in semantic/syntactic processing that are recruited equally by both the high- and low-demand conditions in the contrasts that were included in this meta-analysis. For example, there may well be syntactic operations that are necessary for comprehension that would be seen in a contrast between sentences and a lower level word list baseline, but that are equally recruited for sentences with different levels of syntactic complexity. This issue is particularly salient when it comes to implications for regions that were *not* identified by this analysis, such as the anterior temporal lobe as it leaves open the possibility that these regions are indeed recruited for semantic/syntactic aspects of comprehension, but that their contribution is relatively

consistent across different types of linguistic input is not significantly modulated by the presence of ambiguity/complexity. In this regard, it is worth noting that performance of semantic dementia patients is modulated by the specificity of information required in semantic processing tasks (Adlam et al., 2006) and this corresponds to higher activation of bilateral anterior fusiform regions in normal participants with a requirement for specific semantic information (Rogers et al., 2006), which suggests that this region does index difficulty of the kind considered in the meta-analysis. However, as mentioned earlier, interpretation of the absence of anterior temporal activation is always complicated by the susceptibility artefact of this region, and indeed the aforementioned specificity effects have only been obtained using PET.

The suggestion that our analysis may miss out on core comprehension regions also emphasises, first, the need to consider the results of this meta-analysis in conjunction with other meta-analysis approaches that identify low-level brain regions involved in language comprehension (Turkeltaub & Coslett, 2010). Second, the results should also be interpreted in the light of results from studies using non-linguistic stimuli that emphasise that at least some of the areas identified here are likely to be playing relatively-general cognitive control roles that are not specific to the domain of language comprehension (Jefferies, 2013; Novick et al., 2009; Novick et al., 2005). Third, it is important to consider whether some of the observed clusters do not reflect brain regions that are actively engaged in the semantic/syntactic processes of interest, but instead reflect a down-stream consequence of having attended to a 'difficult' stimulus, such as additional attentional resources being devoted to subsequent processing (cf., Binder et al., 2009, and Davis & Rodd, 2011, for further discussion). This issue is a particular concern when observing activations

in peri-auditory regions, which seem unlikely to be engaged in high-level semantic/syntactic computations. This issue is a pervasive problem in the interpretation of fMRI data, and we suggest that the causal contribution of these brain regions needs to be explored using alternative methods such as Transcranial Magnetic Stimulation (Silvanto & Pascual-Leone, 2012).

One final important contribution that can be made by meta-analyses of this type is their ability to highlight weaknesses in the current literature in terms of the distribution of different approaches that have been used to study particular theoretical questions. Our analysis highlighted that studies examining semantic and syntactic processing tend to use markedly different experimental manipulations (Table I). The syntax studies mainly choose complexity manipulations, while no semantic studies use complexity manipulations. This difference in experimental approach between the two fields is somewhat problematic for interpreting our results in the syntax - semantic contrast, as is it possible that differences on this contrast reflect, to some extent, a difference being driven by differences in the experimental methods being used. But more importantly, this result emphasizes the areas of relative paucity in the experimental literature and we are hopeful that this finding may stimulate future research to use those particular combinations of linguistic contrast and experimental manipulation that are relatively unrepresented in the current literature. We are also hopeful that as the number of relevant studies increases meta-analyses will be possible that move beyond the relatively crude categories of ‘semantic’ and ‘syntactic’ processing used here, and instead explore differences within these categories, for example between the initial activation of semantic representations and the subsequent higher-level operations that act to combine word meanings together to construct sentence meanings.

4.5. Summary

This meta-analysis has produced a number of noteworthy findings. First, it confirmed the critical role of the posterior LIFG in processing semantic and syntactic aspects of language. However the results only provide partial support for the anterior-posterior dissociation in this region that has become widely discussed in the literature, such that syntactic processing is primarily associated with posterior LIFG while semantic processing is primarily associated with anterior LIFG (e.g., Friederici, 2012; Hagoort, 2005). While the contrast between studies of syntax and studies of semantics revealed a significant cluster within posterior LIFG, the reverse contrast revealed no clusters within the LIFG that were more strongly associated with semantic processing. Perhaps most strikingly, the highest ALE score in the semantics-only cluster was found in pars opercularis, which is often associated with syntactic processing.

Our results highlight the need for further work to determine how best to characterise the specific functions of LIFG's sub regions (cf., Rodd et al., 2012; Wright et al., 2011). In particular, we suggest that studies are needed that directly contrast semantic and syntactic processing using experimental designs that aim to hold all other processing demands constant (Rodd et al., 2010). Such studies will allow for testing of claims in the literature of LIFG fractionation on the basis of linguistic information. Future work is also needed to relate this literature on how the semantic and syntactic aspects of words and sentences are processed with the idea that posterior LIFG is primarily associated with phonological processing (Gold et al., 2005; Gough et al., 2005; Katzev, Tuescher, Henning, Weiler, & Kaller, 2013). One possibility is that the types of semantic and syntactic manipulations that are the focus of the current study require listeners/readers to conduct additional processing on

representations held in posterior LIFG that are primarily phonological in nature (e.g., phonological working memory).

The second important finding is the clear emphasis on the *posterior* temporal lobe for both semantic and syntactic processing. This finding is in conflict with models that emphasize the role of the superior anterior temporal lobe in processing sentence-level semantics and syntax (e.g., Friederici, 2012). These two findings highlight the need for future research on this topic, which can also feed into larger scale meta-analyses to provide further information on areas reliably associated with syntactic and semantic processing and the key factors that mediate activation in these areas.

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(Papers marked * were included in the meta-analysis)

Figure captions

Figure 1

ALE meta-analysis clusters for the all 54 semantic and syntactic studies. ALE scores are indicated in the legend.

Figure 2

ALE clusters for the semantic (red) and syntactic (green) studies separately, and their overlap (yellow).

Figure 3

Results of the subtraction analyses for semantic > syntactic studies (red) and syntactic > semantic (green).

Figure 4

Results of the subtraction analyses with the omission of the studies using an anomaly manipulation, semantic > syntactic studies (red) and syntactic > semantic (green).

Localising semantic and syntactic processing in spoken and written language comprehension: An Activation Likelihood Estimation meta-analysis

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Abstract

We conducted an Activation Likelihood Estimation (ALE) meta-analysis to identify brain regions that are recruited by linguistic stimuli requiring relatively demanding semantic or syntactic processing. We included 54 functional MRI studies that explicitly varied the semantic or syntactic processing load, while holding constant demands on earlier stages of processing. We included studies that introduced a syntactic/semantic ambiguity or anomaly, used a priming manipulation that specifically reduced the load on semantic/syntactic processing, or varied the level of syntactic complexity. The results confirmed the critical role of the *posterior* left inferior frontal gyrus (LIFG) in semantic *and* syntactic processing. These results challenge models of sentence comprehension highlighting the role of *anterior* LIFG for semantic processing. In addition, the results emphasise the posterior (but not anterior) temporal lobe for both semantic and syntactic processing.

Key words: Syntax, Semantics, Neuroimaging, Meta-analysis, Methodology, fMRI

1. Introduction

The task of understanding the meaning of a sentence has many component parts. Readers and listeners must retrieve the meaning of each individual word and they must also combine words according to the sentence's syntactic structure to determine how the words relate to each other (e.g., "the boy kissed the girl" vs. "the girl kissed the boy"). In addition, they must use each word's meaning to constrain the precise interpretation of other words in the sentence (e.g., the meaning of the word "bark" in "the bark of the dog" versus "the bark of the tree"). A large number of neuroimaging studies have implicated, with a relatively high level of consistency, several core brain regions as being important for these semantic and syntactic aspects of sentence comprehension (Friederici, 2012; Price, 2012). These regions include, but are not restricted to, left Inferior Frontal Gyrus (LIFG) and anterior and posterior temporal regions.

However, despite the relatively large number of published papers on this topic the field has not yet reached a consensus on several key issues. For instance, Friederici (2012) has outlined a model of spoken language comprehension that emphasizes the role of a ventral pathway that emerges anteriorly from Heschl's Gyrus in constructing the meaning of sentences. Here, sound-to-meaning mapping is localised in the portion of the Superior Temporal Gyrus (STG) that is anterior to Heschl's Gyrus, while a more anterior region of the superior temporal cortex performs general combinatorial processes involved in processing syntactic phrase structure and in combining word meanings. In contrast, others have emphasized the role of the *posterior* portion of the inferior or middle temporal gyri for the function of accessing word meanings on the basis of their spoken form (Hickok & Poeppel, 2007; Poeppel, Emmory, Hickok, & Pylkkanen, 2012; Rodd, Johnsrude, & Davis, 2012) and for

syntactic processing of sentences (e.g., Griffiths, Marslen-Wilson, Stamatakis, & Tyler, 2013; Tyler et al., 2011; 2014).

Disagreement also exists regarding the functional organization of LIFG. Friederici (2012) argues for a strict dissociation on the basis of the linguistic nature of the information to be processed, namely that the frontal operculum and pars opercularis (BA44) sub serve syntactic processing, while the more anterior regions of pars triangularis and pars orbitalis (BA 45 and 47) support semantic processing. Others have suggested a more graded distinction along these lines, such that semantic processing is primarily associated with a more anterior portion of the LIFG compared with syntactic processing, but with substantial overlap in function reflecting the interactive nature of the underlying cognitive processes (Hagoort, 2005). Under this view, the most posterior portion of the LIFG is primarily associated with phonological aspects of comprehension (Gold, Balota, Kirchhoff, & Buckner, 2005; Gough, Nobre, & Devlin, 2005). In contrast, other authors have argued that there is *no* clear dissociation between semantic and syntactic processing within frontal cortex (Rodd, Longe, Randall, & Tyler, 2010) or that activation of this region varies primarily as a function of task demands (Wright, Randall, Marslen-Wilson, & Tyler, 2011). Similarly, the influential conflict resolution account (Novick, Kan, Trueswell, & Thompson-Schill, 2009; Novick, Trueswell, & Thompson-Schill, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) of LIFG function, proposes that posterior LIFG (BA44/45) plays a general role in resolving competition between multiple activated representations for syntactic as well as semantic aspects of comprehension (Novick et al., 2005).

This lack of consensus is firstly due to inconsistencies in published results that may be due to heterogeneity in experimental design across studies. For example,

Dapretto and Bookheimer (1999) report a dissociation between the recruitment of anterior LIFG for semantic processing and posterior LIFG for syntactic processing, while Rodd et al. (2010) report that semantic *and* syntactic manipulations activated the same region of posterior LIFG. When combined with activation of this area during phonological processing (e.g., Rumsey et al., 1997), this latter finding implicates the posterior LIFG (at least) as a multifunctional region. This inconsistency is hard to interpret because these two studies that contrast semantic and syntactic processing differ both in terms of multiple important properties of the stimuli used (visual vs. auditory; words vs. sentences), and also in the tasks used (semantic judgment tasks vs. sentence comprehension). This heterogeneity is typical of the field and illustrates a recurrent problem facing researchers when they try to evaluate the likely cause of discrepancies between individual studies, and the extent to which some findings might result from the limitations of particular experimental paradigms. For example, some researchers (Davis & Rodd, 2011) have raised concerns about the reliance of the field on paradigms that study semantic or syntactic processing by introducing a semantic or syntactic anomaly (e.g., Friederici & Kotz, 2003; Kuperberg et al., 2000). These studies typically assume that by disrupting one specific linguistic property of a sentence it is possible to isolate the brain regions involved in that aspect of processing. In contrast to the ERP paradigms that have used this ‘anomaly’ approach with great success to reveal the time course of sentence processing, fMRI paradigms rely on a slow haemodynamic response that smears together in time participants’ initial response to an anomaly with subsequent processes that are triggered by their detection of the anomaly. For example, when participants encounter a syntactic anomaly, they may engage in additional semantic processes as they try and make sense of what they have read/heard. Alternatively, they may respond to some

anomalies by “giving up” and thus reducing the extent to which both semantic or syntactic information is processed (Kuperberg et al., 2000). Thus it is not clear whether this paradigm can successfully dissociate these two aspects of sentence processing, and whether findings will necessarily be replicated using alternative approaches.

A second reason for the lack of consensus in the field is that each individual study is usually (deliberately) restricted to look at responses to stimuli from a particular domain (auditory vs. visual) or that contain ambiguities or anomalies of a very particular type. Furthermore, given the combinatorial nature of syntax and the wide variety of syntactic constructions that are permitted in natural language, each experiment necessarily samples only a limited range of types of possible sentence structures from the vast possible range of linguistic constructions. This feature of experimental designs can make it difficult to determine the extent to which results should be generalised to other types of stimuli or to other linguistic operations.

We addressed these two limitations by integrating the results across multiple studies in a formal meta-analysis. This approach allowed us to determine which results are consistent across a range of experimental approaches, and which results are more likely to reflect idiosyncratic aspects of a particular study or experimental approach. We expected that this meta-analysis would enable us to identify which areas might be consistently engaged in semantic and syntactic processing across modality of input (auditory/visual) over a wide variety of experimental manipulations and behavioural tasks.

Several published meta-analyses address issues in language comprehension, for instance, focusing on processing at the level of single words (Turkeltaub, Eden, Jones, & Zeffiro, 2002), intelligibility processing at word and sentence level (Adank, 2012a),

semantic processing in general (Binder, Desai, Graves, & Conant, 2009), and the role of the left hemisphere in processing phonology, semantics, and sentence processing (Vigneau et al., 2006). However, there are no published meta-analyses that directly contrast semantic and syntactic processing. The Vigneau et al., (2006) analysis compares contrasts that are categorised as ‘semantic processing’ or ‘sentence processing’, but the latter set of contrasts include those that inevitably also load on semantic aspects of sentence processing (e.g., sentences vs. unlinked words; sentences with high vs. low mental imagery content). In addition, the Vigneau et al. analysis does not include the relatively large set of studies that have used semantic ambiguities/anomalies to investigate semantic processing at a sentence level. Therefore, we aimed to map out the neural network associated with how language users resolve two types of higher-level problems during language comprehension, namely computing the meanings of words (in isolation or in context) and the syntactic structures of sentences. Importantly, we only included studies that explicitly varied the processing demand on the semantic/syntactic aspects of the linguistic material being processed, for example by the introduction of a semantic/syntactic ambiguity, complexity or anomaly, or by including a priming or relatedness manipulation that specifically reduced the processing load on these aspects of comprehension. We restricted our analysis to studies that include contrasts of this type while holding constant (i) the processing demands on lower-level form based processes and (ii) the task being performed. While our primary interest is in how these semantic/syntactic processes operate at the level of the sentence, we did not restrict the analysis to studies that use sentence materials, but also included studies using single words (or word pairs or triplets) where the experimental contrasts are clearly semantic in nature (e.g., semantic priming).

We used the Activation Likelihood Estimation (ALE) method (Laird et al., 2005; Turkeltaub et al., 2002), an objective and quantitative technique for meta-analysis of coordinates from neuroimaging results. ALE can be used to determine the overlap between coordinates obtained from neuroimaging studies by modelling them as probability distributions centred at the reported coordinates. The meta-analysis applies ALE to coordinates collected from neuroimaging studies investigating semantic or syntactic processing (or both).

ALE was first used to identify the network of brain regions that are consistently activated by these semantic/syntactic aspects of language comprehension. We anticipate that this analysis will reveal areas commonly identified in studies on semantic and syntactic processing, but may also reveal additional regions that may not previously have been the focus of extensive discussion. Second, we determined how activation in this network is modulated the linguistic nature of the experimental contrast (syntax vs. semantics).

The key contrast between studies that include semantic and syntactic manipulations could produce a range of different outcomes. Friederici (2012) emphasizes the differences between the networks of brain regions thought to be involved in these two key aspects of sentence comprehension: syntactic processing is most strongly associated with superior anterior temporal cortex, the frontal operculum, pars opercularis and the posterior portion of pars triangularis, while sentential semantic processing is associated with the more anterior portion of pars triangularis and pars orbitalis. This account therefore predicts that the contrast between these two types of linguistic manipulations should produce clear dissociations within these regions. In contrast, other authors have emphasized the commonalities in the regions that are activated by these two aspects of sentence

comprehension and suggest that differences in the nature of the task demands may be the key factor in producing variation in patterns of LIFG responses (Rodd et al., 2012; Rodd et al., 2010; Wright et al., 2011).

In summary, the aim of this meta-analysis was to first identify the set of brain regions that are involved in semantic or syntactic aspects of comprehension, by contrasting responses to stimuli that place specific increases on these aspects of comprehension with simpler linguistic stimuli.

2. Method

2.1. Selection of literature studies

We selected neuroimaging studies investigating language comprehension at post-lexical levels using Pubmed. We searched the Pubmed online database for studies using the keywords: “speech”, “reading”, “auditory”, “comprehension”, “fMRI”, “PET”, “narrative”, “sentence”, “word”, “neuroimaging”, “priming”, “repetition suppression”, “ambiguity”, “anomaly”, “incongruent”, “congruent”, “syntactic”, “complexity”, “context” and appropriate combinations of these keywords. In addition, we collected additional papers by searching for prominent researchers in the field.

2.2. Inclusion and exclusion criteria

Papers were included that fulfilled the following criteria: (i) neural responses were collected using fMRI or PET, (ii) only healthy, neurotypical subjects with intact hearing and no known neurological or psychiatric disorders were tested, (iii) the experiments contained conditions that explicitly manipulated the processing load on syntactic or semantic processing in spoken or written modalities, (iv) the paper included a table with foci for a comparison between conditions in which participants were processing stimuli that were more demanding to process versus those that were

less demanding to process, where the ‘demanding’ manipulation was either semantic or syntactic in nature, (v) the stimuli consisted of words or word pairs, word triplets, sentences, stories, or narratives; and (vi) results were reported at a group-level in a stereotactic 3-coordinate system. The following criteria were used to exclude papers from the analysis: (i) single subject studies, and (ii) studies that report only results from a pre-specified region-of-interest (ROI) analysis, or (iii) studies that contrasted meaningful stimuli with meaningless stimuli (e.g., words vs. pseudo-words), (iv) studies where the two critical conditions differed in the processing load on pre-semantic lexical access processes (e.g., primed vs. un-primed words in a single modality, i.e., repetition priming), (v) studies where the contrasts were likely to result in substantial differences in *both* semantic and syntactic processing (e.g., sentences vs. word lists, and sentences vs. ‘jabberwocky’ sentences for which both syntactic and combinatorial semantics are disrupted).

2.3. ALE methods

The ALE analysis was implemented using GingerALE 2.3 (www.brainmap.org), using the algorithm proposed in Turkeltaub et al. (2012). Coordinates collected from studies reporting coordinates in Talairach space were converted to MNI space using the `tal2icbm_spm` algorithm implemented in the GingerALE software (www.brainmap.org/ale).

GingerALE first computes modelled activation maps for each set of foci per included study. These foci are modelled as Gaussian distributions and merged into a single 3-dimensional volume. GingerALE uses an uncertainty modelling algorithm to empirically estimate the between-subjects and between-templates variability of all included foci sets. Second, ALE values are computed on a voxel-to-voxel basis by taking the values that are common to the individual modelled activation maps.

GingerALE constrains the limits of this analysis to a grey matter mask that was used to define the outer limits of MNI coordinate space, which excludes most white-matter structures (Eickhoff, Heim, Zilles, & Amunts, 2009). Furthermore, GingerALE does not take into account spatial smoothing kernels from individual papers, but determines spatial smoothing based on the number of participants in each experiment. Therefore, the number of participants was verified in each paper and participant numbers in Table I represent participants included in the neuroimaging analysis of each paper only (some studies excluded participants due to motion artefacts or technical difficulties).

We first ran a series of ALE analyses on (i) the complete set of studies and (ii) the two critical subsets of studies (syntactic, semantic) to explore the network of areas associated with each set and to examine the overlap between networks. These single studies were corrected for multiple comparisons using the FDR (false discovery rate) pID method at $q < 0.001$, voxel wise (default setting $q < 0.05$), using a cluster extent of 200mm^3 (default), following (Adank, 2012a, 2012b).

Second, we performed analyses that directly contrasted the ALE maps constructed above for the two key factors: linguistic type (semantic vs. syntactic). The first step consisted of running a series of two ALE analyses for (i) semantic contrasts, (ii) syntactic contrasts. These analyses were corrected for multiple comparisons using the FDR pID method at $q < 0.05$, voxel wise (default setting), using a cluster extent of 200mm^3 . In a second step, we used the thresholded ALE maps from the first step to run a series of subtraction analyses. These subtraction analyses were conducted using a FDR pID method at $q < 0.05$, voxel wise, again using a cluster extent of 200mm^3 , while the null distributions of the ALE scores were based on Monte Carlo simulations with 10,000 iterations. The ALE statistical maps for each subtraction analysis were

converted to voxel-wise probability maps based on these null distributions. The Mango software package (<http://ric.uthscsa.edu/mango/>) was used to view the resulting activation maps and all results were overlaid on a single MNI template available in Mango (Colin27_T1_seg_MNI.nii). We report only results for clusters that listed two or more experiments.

We used the Anatomy ToolBox for our anatomical localisation (Eickhoff, Heim, Zilles, & Amunts, 2006; Eickhoff et al., 2007; Eickhoff et al., 2005) in SPM8 (Wellcome Imaging Department, University College London, London, UK), as it provides localisation based on probabilistic maps included for several key areas of our study, including LIFG (Amunts et al., 1999), as expressed as a probability (in %) of a specific coordinate being located in Brodmann Areas (BA) 44 or 45.

--- *Insert Table I about here* ---

3. Results

3.1. Summary of included studies

We conducted the meta-analysis on studies that met the criteria for comprehension of semantic and syntactic processes. The studies in Table I were based on results from 54 fMRI experiments, 957 subjects, and 320 foci. No PET studies met the criteria. Stimuli were spoken or written single words, word pairs or triplets, sentence fragments, sentences, or narratives, and a variety of tasks were used. Finally, we also coded whether each experiment was conducted in a spoken or written modality, whether syntactic or semantic processing was examined, as well as the type of experimental manipulation used.

Experimental manipulations used across the studies were classified into six categories: ambiguity, anomaly, complexity, relatedness, cross-modal priming, and other. Although these classifications are not used in the analysis stage they provide an

important overview of the distribution of approaches used in the field, and in particular how these might differ across the categories of semantic and syntactic studies. Ambiguities were defined as stimuli for which multiple different semantic/syntactic representations were (temporarily) consistent with all or part of the linguistic input, but where it was possible for the listener/reader to resolve this ambiguity and produce a coherent, meaningful representation. Anomalies were defined as stimuli that contained an incongruous element that could not be integrated into the overall representation of the stimulus. A manipulation was classified as ‘complexity’ if the two contrasts differed in the complexity of the semantic/syntactic representation. In practice, this classification was only used for cases where the stimuli differed on the complexity of the resulting *syntactic* structure, as there were no equivalent studies of semantic complexity. A study was classified as ‘relatedness’ if it contrasted semantically related words/word pairs or sentences with semantically unrelated word pairs. Studies were classified as ‘cross-modal priming’ if they repeated semantic or syntactic stimuli in two different modalities, e.g., presenting a word/concept auditorily and as a picture. Some remaining studies did not fit into a single coherent category and were classified into a more general category of ‘other’, which included one experimental manipulation, namely establishing the contrast between sentences with high- or low-cloze probability. Table I shows the distribution of studies across the factors linguistic task (syntax vs. semantics) and stimulus presentation modality (reading vs. listening). Table I reveals a sharp difference in the main manipulations used by studies examining semantic or syntactic processing. The most striking difference is that 20 of the 28 syntax studies used a complexity manipulation (e.g., more versus less complex syntax), while no semantics studies

make use of this experimental manipulation. Instead, the included semantics studies use a wider variety of manipulations.

3.2. Main Comprehension Network

The main analysis included the data from all studies to identify regions that were more active for semantically/syntactically demanding stimuli. Figure 1 shows the main network of ALE clusters. Analysis of the experiments in Table I resulted in the ten significant clusters in Table II. The peaks of these clusters were distributed across left IFG (the central coordinates of the cluster were located in left POp and extended into Precentral Gyrus, PG, and PTr), left MTG extending into left STG, right IFG (POp and PTr), Precuneus, left IPL, left Inferior Temporal Gyrus (ITG), and left POrb (pars orbitalis).

--- Insert Table II and Figure 1 about here ---

3.3 Syntactic vs. Semantic Processing

We looked at the individual ALE clusters for (i) semantic and (ii) syntactic processing. The 54 studies were split into groups depending on whether they included a semantic contrast (26 studies, 167 foci) or a syntactic contrast (28 studies, 153 foci). Demanding semantic processing was associated with six ALE clusters (Table III and Figure 2), located in left pars opercularis (POp) of IFG, extending anteriorly into pars triangularis (PTr), left STG, left ITG, and left POrb. The analysis of studies addressing demanding syntactic processing resulted in eight ALE clusters, in Left POp (extending to PTr and left insula), Precuneus, left MTG, left PG, left SMA, left IPL, and left Supramarginal Gyrus (SMG).

--- Insert Table III and Figure 2 about here ---

Next, we directly compared the results from syntactic and semantic studies in a subtraction analysis using the procedure and significance levels outlined in section

2.3. GingerALE reported nine clusters for the contrast Semantics > Syntax, of which four contained the minimum of two or more contributing experiments (Table IV; Figure 3). The clusters were located in left ITG extending into Fusiform Gyrus (FFG), right Insula, and Left Superior Frontal Gyrus (SFG). GingerALE reported seven clusters for the contrast Syntax > Semantics, of which five contained two or more contributing experiments, located in left Superior Parietal Lobule (SPL) extending to Precuneus, left Middle Occipital Gyrus (MOG) extending into SPL and AG, left Superior Medial Gyrus (SMedG), left Insula extending into left POp, and left SMG extending into IPL.

--- Table IV and Figure 3 about here ---

Finally, we repeated the semantic vs. syntactic subtraction analyses with the omission of the 10 studies that used an anomaly manipulation (cf. Table I), which has been criticised by some authors for not strictly dissociating syntactic and semantic aspects of processing (Davis & Rodd, 2011). The remaining 44 studies (257 foci) were split into groups depending on whether they included a semantic (20 studies, 124 foci) or a syntactic contrast (24 studies, 133 foci). However, these exclusions did not result in an enhanced dissociation between the two forms of processing. The subtraction analysis showed five clusters for Semantics > Syntax, of which two listed two or more experiments. The first was located in left STG extending to MTG and the Rolandic Operculum and the second was located in left ITG extending into FFG (Table V, Figure 4). The subtraction analysis showed nine clusters for the contrast Syntax > Semantics, of which three contained two or more contributing experiments, located in left SPL extending to Precuneus, left POp in LIFG extending into the insula, and left PG.

--- Table V and Figure 4 about here ---

4. Discussion

The present study aimed to delineate the network of brain regions associated with processing semantic and syntactic aspects of language comprehension in a formal meta-analysis across 54 studies. The present meta-analysis differs from previous analyses (Adank, 2012a; Binder et al., 2009; Visser, Embleton, Jefferies, Parker, & Lambon-Ralph, 2010) in that we focused on how the linguistic system deals with comprehensible yet demanding linguistic stimuli and only included contrasts that specifically compared two types of meaningful stimuli that differed on the cognitive load placed on either semantic or syntactic aspects of comprehension. The initial analysis (Figure 1, Table II) highlighted a number of brain regions, discussed below, as being activated by these semantic or syntactic aspects of comprehension.

4.1. *Left Inferior Frontal Gyrus*

The largest cluster in the main analysis had its peak within pars opercularis, and extended anteriorly into pars triangularis, inferiorly into pars orbitalis and posteriorly and dorsally into the Precentral Gyrus (Figure 1; Table II). Subsequent analyses confirmed that both syntactic and semantic contrasts produced large (and partially overlapping) clusters within the posterior LIFG (Figure 2; Table III). In the case of syntax, the cluster is centred on pars opercularis and does not contain sub peaks within either pars triangularis or pars opercularis. In contrast, for semantics although the peak voxel is again within pars opercularis the cluster extends more dorsally than the syntactic cluster, and also includes a more anterior sub peak within pars triangularis as well as a separate small cluster in pars orbitalis.

This qualitative pattern seen in Figure 2 is confirmed, to some extent, by the direct subtraction contrast between syntax and semantics (Table IV; Figure 3), which

reveals a cluster with peaks in pars opercularis and the insula, confirming that this most posterior/ventral aspect of the main cluster is preferentially activated in studies of syntactic processing. This particular finding is (taken in isolation) consistent with the claim made by Friederici (2012), who argues that the frontal operculum and pars opercularis (BA44) subserve syntactic processing, and Hagoort (2005)'s claim that BA 44 and 45 make a particular contribution to syntactic processing. The reverse contrast, between semantic and syntactic processing is also somewhat compatible with these accounts: a corresponding 'semantic effect' is seen within both pars triangularis and pars orbitalis (Table IV), although it is important to emphasise that these effects only emerge when a relatively lenient statistical threshold is applied. However, although these isolated peaks can perhaps be taken evidence to support the anterior-posterior dissociation between semantic and syntactic aspects of processing there are two important caveats to this conclusion. First, the peak of the semantic-only cluster (Table III) lies within pars opercularis (i.e. in *posterior* LIFG), suggesting that although anterior LIFG may be additionally recruited by these studies of semantic processing compared with syntactic processing it appears that it is the more posterior region that is mostly strongly associated with *both* semantic and syntactic processing. This overlapping recruitment of posterior LIFG is most clearly shown in Figure 2. This strong association between posterior LIFG and semantic processing is inconsistent with those accounts that assert that such aspects of comprehension are primarily associated with anterior LIFG (Friederici, 2012; Hagoort, 2005). The finding that *both* semantic and syntactic aspects of comprehension are primarily associated with activation in the posterior LIFG is consistent with the influential conflict resolution account (Novick et al., 2009; Novick et al., 2005; Thompson-Schill et al., 1997) of LIFG function, which suggests that the posterior region of the LIFG

(BA44/45) plays a crucial role in resolving competition between activated representations to support the selection of a single representation. While this account has primarily been discussed with respect to *semantic* processing, these authors have explicitly noted the importance of these cognitive control processes for syntactic aspects of comprehension (Novick et al., 2005). In contrast to this proposed role for the *posterior* LIFG in conflict resolution, Badre and colleagues specifically attribute the *anterior* LIFG (pars orbitalis) to the controlled retrieval of semantic information from long-term memory (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2007). This process is required when stimulus-driven cues are insufficient to activate information relevant to one's goal or task, such as in the case of a semantic decision where two stimuli are weakly rather than strongly associated.

Our findings of posterior LIFG activation for both semantic and syntactic aspects of language comprehension can most easily be interpreted in this framework by assuming that resolving competition between activated representations is a core cognitive process that is routinely engaged when comprehending linguistic input that is relatively challenging to understand due to either its semantic or syntactic properties. For example in the case of a semantic/syntactic ambiguity it is clear that selection between multiple representations would be required, and it is at least plausible that the other manipulations such as the introduction of anomalies or syntactic complexities might result in more complex linguistic representations that necessitate increased demands on the processes that can select between the different pieces of information that are initially activated in response to each isolated word. In contrast, the limited extent of the anterior LIFG activation in the main contrast (Figure 1; Table II) and for the semantic condition alone (Figure 2) might indicate that 'controlled retrieval' plays a more limited role in the language comprehension

processes that are the focus of the studies included in this meta-analysis. Further studies are clearly needed to reveal the specific cognitive conditions that are required for anterior LIFG involvement in language comprehension.

An alternative account of the LIFG's role in language comprehension comes from Hagoort and colleagues (Hagoort, 2005, 2013; Hagoort, Baggio, & Willems, 2009). According to this theory, the LIFG constitutes a unification space that combines basic units of information to form larger complex representations of a sentence or discourse. In contrast to the conflict resolution account, this theory argues that it is combinatorial demands that drive activation in this region rather than conflict or selection load per se. According to this account, selection is merely one aspect of unification. This account is consistent with the findings of LIFG clusters found across a range of semantic and syntactic contrasts: all the ambiguity, anomaly, complexity and priming manipulations included in this meta-analysis would be predicted to directly increase the demands on these unification processes.

However, as previously discussed, the current data are not fully consistent with the unification account, which explicitly proposes functional specialisation across the LIFG such that semantic information is preferentially processed by pars orbitalis and pars triangularis, syntactic information by pars triangularis and pars opercularis and phonological processes by pars opercularis and premotor cortex. This fractionation is not consistent with our findings that semantic processing is primarily associated with *posterior* LIFG (pars opercularis/triangularis).

More generally, our results indicate that it may be premature to suggest that *any* region of the LIFG is specialised for semantic aspects of language comprehension. We suggest that the view that such an association exists has arisen primarily because of the focus in the semantic processing literature on explicit

semantic decision tasks and which load heavily on controlled retrieval of semantic information from long-term memory (e.g., Badre et al., 2005; Badre & Wagner, 2007; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Equivalent explicit judgement tasks are relatively rare in the syntactic processing literature. We suggest that the absence of extensive anterior LIFG clusters in this meta-analysis reflects our focus on studies that manipulate the difficulty of language *comprehension* processes, rather than comparing explicit semantic judgement tasks that vary on *task* difficulty. We suggest that to establish with any degree of certainty whether the function of the LIFG can be fractionated on the basis of the linguistic category of the information being processed requires additional studies which directly compare semantic and syntactic processing, while holding constant demands on processes such as selection, retrieval and working memory (see Rodd et al., 2010, for one attempt at such an approach).

Finally, it is important to consider the apparent lateralisation of this frontal activation. While the main analysis does reveal a right lateralised cluster of activation with sub peaks in both part opercularis and triangularis (Figure 1, Table II), this is very considerably reduced both in terms of extent and ALE value compared with its left hemisphere homologue, and it does not show a significant cluster in the separate analyses of semantic or syntactic processing or the direct contrast between them. The involvement of right hemisphere regions in comprehension is of particular theoretical interest given the relatively strong claims that have been made by some authors that it plays a critical role in maintaining non-selected word meanings in case subsequent reinterpretation is needed (e.g., Faust & Chiarello, 1998; Faust & Gernsbacher, 1996). The current approach, which is only able to reveal regions that are consistently recruited by a range of different semantic/syntactic computations,

does not provide a strong test of such very specific claims about the functional contribution of right hemisphere regions. All that can be concluded from these results is that there is evidence, albeit relatively weak, for the involvement of this region, and that future work is needed to determine the precise contribution of the right IFG.

4.2. Left temporal lobe

The second large cluster in the main analysis has its peak in posterior MTG, but extends superiorly (and anteriorly) into the mid STG (Figure 1; Table II). In contrast, there are no significant clusters in the more anterior regions of the superior temporal lobe that have been highlighted by some current accounts (e.g., Friederici, 2012) as being critical for sentential levels of processing for both semantic and syntactic information. Therefore these results seem more consistent with accounts that emphasize the role of the *posterior* portion of the inferior or middle temporal gyri in comprehension (Griffiths et al., 2013; Hickok & Poeppel, 2007; Mummery et al., 1999; Poeppel et al., 2012; Rodd et al., 2012; Tyler et al., 2011; Wilson et al., 2014).

The analyses that focus separately on semantic and syntactic processing help to clarify the roles of these different sub regions within the temporal lobe. The mid STG is only observed in the analysis of semantic processing, but is absent in the analysis of syntactic processing (Table III; Figure 2), and indeed shows more activation for semantic process albeit at a relatively low level of significance (Tables IV and V; Figure 3). This finding is somewhat surprising as this region is primarily associated with relatively low level auditory processing, rather than higher-level semantic aspects of processing. The sets of semantic and syntactic studies included here were relatively well balanced in terms of the proportion of studies that used auditory materials (semantics: 38% vs. syntax: 43%, see Table I) so it is unlikely that this finding reflects a simple selection bias. Given the wealth of evidence to support the

role of these per-auditory regions in speech perception not comprehension (Deschamps & Tremblay, 2014; Sætrevik & Specht, 2012; Turkeltaub & Coslett, 2010), we speculate that that this region is not actively engaged in the semantic processes of interest, but instead reflect a down-stream consequence of having attended to a ‘difficult’ stimulus, such as additional attentional resources being devoted to subsequent processing (cf., Binder et al., 2009, and Davis & Rodd, 2011, for further discussion). Further research is needed to determine what specific properties of hard-to-comprehend linguistic stimuli trigger the engagement of such regions and why, for this set of studies, this is preferentially occurring for the studies focusing on semantic processing.

In contrast to the semantic bias seen for STG, the posterior MTG region identified in the main analysis seems to be primarily associated with syntactic processing (Table III; Figure 2). This is consistent with theoretical accounts that attribute this region a key role in syntactic processing. (e.g., Griffiths et al., 2013; Tyler et al., 2011; Wilson et al., 2014). However it is important to note that although this region is seen only in the syntactic analysis and not the semantic analysis, it does not show a significant difference in its response to these two forms of processing (Tables III and IV; Figure 3), and so we remain cautious in attributing this region a role that is specific to syntactic processing. An alternative account of this region’s involvement in sentence comprehension, which is compatible with the current results, is that this region is only recruited for cases where the comprehended needs to reinterpret a part of a sentence that was initially misparsed (Rodd et al., 2012).

Finally, a third region of the left temporal lobe that emerges from these analyses as having a key role in comprehension is the left posterior ITG. Interestingly, this region is *only* significantly associated with semantic and not syntactic activation, and

the direct contrast between these two aspects of comprehension shows a large cluster of activation centred on the ITG but also including sub peaks within the fusiform gyrus. Parts of left fusiform gyrus have been associated with the representation of written word forms (e.g., Vinckier et al., 2007), but its implication here for both printed and spoken materials is consistent with studies showing activation in response to multiple inputs (Price & Devlin, 2003), concordant with a role for this region in integrating visual, semantic and phonological information (Price & Devlin, 2011). The association we observed between semantic processing and left fusiform gyrus activation also agrees with previous work showing a relationship between semantic errors in picture naming and integrity of BA 37 amongst acute stroke patients (Cloutman et al., 2009). However, the cluster we observed encompasses a large region of cortex and further work is needed to discover the functional roles of any adjacent regions.

It is notable that semantic processing was associated with activation in a relatively posterior part of the fusiform gyrus (BA 37), but no clusters were seen in the adjacent anterior fusiform gyrus (BA 20), which has been associated with multimodal semantic processing (Visser, Jefferies, & Lambon-Ralph, 2010). While posterior fusiform gyrus generates a clear MRI signal, the anterior inferior portions of the anterior temporal lobe are subject to considerable susceptibility artefact, and activation can also be missed when a restricted field of view is used (Visser, Embleton, et al., 2010). Although solutions to this problem have been recently developed (Visser & Lambon Ralph, 2011) many of the studies included here have not been designed to optimise signal in these regions, which renders the absence of its association with semantic processing in the current study difficult to interpret. It should also be noted that a similar issue arises when considering the absence of

activation in anterior superior temporal regions, as MRI signal in BA 38 is also vulnerable, albeit to a lesser extent, to susceptibility artefacts (Devlin et al., 2000). Future work considering the involvement of the anterior temporal regions in sentence level comprehension is therefore required.

4.3. Limitations

The conclusions drawn above need to be considered in the context of some general limitations of our methodological approach. Firstly, we must consider some general limitations of our meta-analysis that are shared by other recent meta-analyses (Luk, Green, Abutalebi, & Grady, 2011; Richlan, Kronbichler, & Wimmer, 2009; Turkeltaub & Coslett, 2010). First, these meta-analysis tools only allow us to consider the main effect of our key variable (i.e. syntax vs. semantics), but do not allow us either to look for interactions with other variables, or to partial out variance due to other potentially confounding variables. For example, the finding of a difference between syntactic and semantic processing in posterior LIFG should be treated with caution, for three reasons. First, we cannot be certain that a ‘syntactic’ cluster truly corresponds to the particular linguistic manipulation that was used in the syntactic studies included in our analysis, and not to some other processing demand that is more likely to be present in the majority of these syntactic studies, compared with the semantic studies. For example, we cannot rule out the possibility that the syntactic manipulations included in these experiments produce an enhanced load on verbal/phonological working memory processes compared with the semantic manipulations, particularly given the greater prevalence of sentence-level stimuli in the syntactic relative to semantic investigations. Any difference found between semantic and syntactic studies may have been affected by the fact that all syntactic studies except for one (Herrmann, Obleser, Karlerlah, Haynes, & Friederici, 2012)

who used two-word utterances) used sentences or sentence fragments, while four of the semantic studies used single words, eight used word pairs or word triplets, and 14 used sentences (Table I). We were not able address this confound, e.g., by examining differences between semantic and syntactic studies without inclusion of the studies using word stimuli, as this would result in comparing a group of 27 experiments with one with 14 experiments, which is not advisable as the power would be too low for the subtraction analysis in GingerALE.

Likewise, when interpreting the observed overlap between the clusters produced by syntactic and semantic studies, it must be kept in mind that the meta-analysis process averages results over multiple studies, which have in turn averaged over individual participants. This approach can potentially lead to adjacent, but separate, clusters of activation, which may vary in precise location across individuals, appearing to overlap. Future studies are needed to determine whether additional functional specialization within the large clusters identified here can be observed within individual participants or in-group analyses with low levels of smoothing.

Perhaps more important than these general limitation of this approach are the issues that arise from our specific choices regarding which contrasts to include. In particular, our choice to only include contrasts between more demanding and less demanding stimuli conditions. This choice was made in order to assure that *all* of the regions we identified are recruited for semantic/syntactic aspects of comprehension and were not associated with lower-level phonological/lexical aspects of comprehension. This relatively selective approach may have had two separate and important consequences. First, it is possible that these analyses may be identifying regions that are not ‘core’ parts of the language processing network, but that are only recruited in response to specific unusual or idiosyncratic aspects of the more

demanding stimuli. Indeed a recent study of semantic ambiguity indicates that some of the posterior frontal and inferior temporal regions highlighted here are *not* routinely recruited by low-ambiguity sentences, having found that these kinds of sentences stimuli did not show increased activation compared with an unintelligible baseline (Vitello, Warren, Devlin, & Rodd, 2014) and some authors have suggested, for example, that portions of the LIFG are *only* recruited during sentence comprehension if the listener/reader is required to reinterpret a sentence (Novick et al., 2005; Rodd et al., 2012). An important point here is that, although these regions may not be automatically or obligatorily recruited for *all* sentences, that does not mean that they should not be considered core language comprehension regions. Natural language is replete with both semantic and syntactic ambiguities as well as syntactic complexity making it highly likely that the brain regions identified in this meta-analysis are necessary components of our comprehension system.

A related, but separate, issue is the possibility that this approach only highlights a subset of the brain regions involved in semantic and syntactic aspects of comprehension, specifically, that it may miss some core language processing regions involved in semantic/syntactic processing that are recruited equally by both the high- and low-demand conditions in the contrasts that were included in this meta-analysis For example, there may well be syntactic operations that are necessary for comprehension that would be seen in a contrast between sentences and a lower level word list baseline, but that are equally recruited for sentences with different levels of syntactic complexity. This issue is particularly salient when it comes to implications for regions that were *not* identified by this analysis, such as the anterior temporal lobe as it leaves open the possibility that these regions are indeed recruited for semantic/syntactic aspects of comprehension, but that their contribution is relatively

consistent across different types of linguistic input is not significantly modulated by the presence of ambiguity/complexity. In this regard, it is worth noting that performance of semantic dementia patients is modulated by the specificity of information required in semantic processing tasks (Adlam et al., 2006) and this corresponds to higher activation of bilateral anterior fusiform regions in normal participants with a requirement for specific semantic information (Rogers et al., 2006), which suggests that this region does index difficulty of the kind considered in the meta-analysis. However, as mentioned earlier, interpretation of the absence of anterior temporal activation is always complicated by the susceptibility artefact of this region, and indeed the aforementioned specificity effects have only been obtained using PET.

The suggestion that our analysis may miss out on core comprehension regions also emphasises, first, the need to consider the results of this meta-analysis in conjunction with other meta-analysis approaches that identify low-level brain regions involved in language comprehension (Turkeltaub & Coslett, 2010). Second, the results should also be interpreted in the light of results from studies using non-linguistic stimuli that emphasise that at least some of the areas identified here are likely to be playing relatively-general cognitive control roles that are not specific to the domain of language comprehension (Jefferies, 2013; Novick et al., 2009; Novick et al., 2005). Third, it is important to consider whether some of the observed clusters do not reflect brain regions that are actively engaged in the semantic/syntactic processes of interest, but instead reflect a down-stream consequence of having attended to a ‘difficult’ stimulus, such as additional attentional resources being devoted to subsequent processing (cf., Binder et al., 2009, and Davis & Rodd, 2011, for further discussion). This issue is a particular concern when observing activations

in peri-auditory regions, which seem unlikely to be engaged in high-level semantic/syntactic computations. This issue is a pervasive problem in the interpretation of fMRI data, and we suggest that the causal contribution of these brain regions needs to be explored using alternative methods such as Transcranial Magnetic Stimulation (Silvanto & Pascual-Leone, 2012).

One final important contribution that can be made by meta-analyses of this type is their ability to highlight weaknesses in the current literature in terms of the distribution of different approaches that have been used to study particular theoretical questions. Our analysis highlighted that studies examining semantic and syntactic processing tend to use markedly different experimental manipulations (Table I). The syntax studies mainly choose complexity manipulations, while no semantic studies use complexity manipulations. This difference in experimental approach between the two fields is somewhat problematic for interpreting our results in the syntax - semantic contrast, as is it possible that differences on this contrast reflect, to some extent, a difference being driven by differences in the experimental methods being used. But more importantly, this result emphasizes the areas of relative paucity in the experimental literature and we are hopeful that this finding may stimulate future research to use those particular combinations of linguistic contrast and experimental manipulation that are relatively unrepresented in the current literature. We are also hopeful that as the number of relevant studies increases meta-analyses will be possible that move beyond the relatively crude categories of ‘semantic’ and ‘syntactic’ processing used here, and instead explore differences within these categories, for example between the initial activation of semantic representations and the subsequent higher-level operations that act to combine word meanings together to construct sentence meanings.

4.5. Summary

This meta-analysis has produced a number of noteworthy findings. First, it confirmed the critical role of the posterior LIFG in processing semantic and syntactic aspects of language. However the results only provide partial support for the anterior-posterior dissociation in this region that has become widely discussed in the literature, such that syntactic processing is primarily associated with posterior LIFG while semantic processing is primarily associated with anterior LIFG (e.g., Friederici, 2012; Hagoort, 2005). While the contrast between studies of syntax and studies of semantics revealed a significant cluster within posterior LIFG, the reverse contrast revealed no clusters within the LIFG that were more strongly associated with semantic processing. Perhaps most strikingly, the highest ALE score in the semantics-only cluster was found in pars opercularis, which is often associated with syntactic processing.

Our results highlight the need for further work to determine how best to characterise the specific functions of LIFG's sub regions (cf., Rodd et al., 2012; Wright et al., 2011). In particular, we suggest that studies are needed that directly contrast semantic and syntactic processing using experimental designs that aim to hold all other processing demands constant (Rodd et al., 2010). Such studies will allow for testing of claims in the literature of LIFG fractionation on the basis of linguistic information. Future work is also needed to relate this literature on how the semantic and syntactic aspects of words and sentences are processed with the idea that posterior LIFG is primarily associated with phonological processing (Gold et al., 2005; Gough et al., 2005; Katzev, Tuescher, Henning, Weiler, & Kaller, 2013). One possibility is that the types of semantic and syntactic manipulations that are the focus of the current study require listeners/readers to conduct additional processing on

representations held in posterior LIFG that are primarily phonological in nature (e.g., phonological working memory).

The second important finding is the clear emphasis on the *posterior* temporal lobe for both semantic and syntactic processing. This finding is in conflict with models that emphasize the role of the superior anterior temporal lobe in processing sentence-level semantics and syntax (e.g., Friederici, 2012). These two findings highlight the need for future research on this topic, which can also feed into larger scale meta-analyses to provide further information on areas reliably associated with syntactic and semantic processing and the key factors that mediate activation in these areas.

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(Papers marked * were included in the meta-analysis)

Figure captions

Figure 1

ALE meta-analysis clusters for the all 54 semantic and syntactic studies. ALE scores are indicated in the legend.

Figure 2

ALE clusters for the semantic (red) and syntactic (green) studies separately, and their overlap (yellow).

Figure 3

Results of the subtraction analyses for semantic > syntactic studies (red) and syntactic > semantic (green).

Figure 4

Results of the subtraction analyses with the omission of the studies using an anomaly manipulation, semantic > syntactic studies (red) and syntactic > semantic (green).

Table I

Table I. The 54 fMRI studies included in the ALE meta-analysis grouped into those exploring semantic processing and those exploring syntax processing. * = no info given.

#	Study	N	Language	Modality	Stimulus	Task	Manipulation	Contrast	Source	Experiment	Foci	FWHM mm ³
Semantics												
1	Bekinstein et al. (2011)	12	British English	auditory	sentences	passive listening	ambiguity	ambiguous > unambiguous	Table 1	1	2	12
2	Grindrod et al. (2008)	15	American English	auditory	word triplets	lexical decision	relatedness	discordant > neutral	Table 3	1	1	6
3	Han et al. (2007)	12	American English	auditory	word pairs	lexical decision	relatedness	unrelated > high connectivity + low connectivity	Main text	1	2	10
4	Kotz et al. (2002)	13	German	auditory	words	lexical decision	relatedness	unrelated > related	Table 4	1	9	*
5	Kuperberg et al. (2000)	9	British English	auditory	sentences	semantic decision	anomaly	anomalous > non-anomalous	Table 5	1	2	10.8
6	Obleser & Kotz (2010)	16	German	auditory	sentences	passive listening + post task	other	low cloze > high cloze	Table 1	1	3	8
7	Rissman et al. (2003)	15	German	auditory	words	lexical decision	relatedness	unrelated > related	Table 2	1	5	6
8	Rodd et al. (2005)	30	British English	auditory	sentences	semantic decision of	ambiguity	high ambiguity > low ambiguity	Table 4	1+2	4	12

						post stimulus probe, passive listening + posttask						
9	Rodd et al. (2010)	14	British English	auditory	sentences	button press after sentence for 50% of sentences	ambiguity	high ambiguity > low ambiguity	Table 3	1	4	8
10	Ruff et al. (2008)	15	British English	auditory	word pairs	relatedness judgment and lexical decision	relatedness	unrelated > related	Table 2	1	9	6
11	Tesink et al. (2009)	42	Dutch	auditory	sentences	passive listening	anomaly	anomalous > non- anomalous	Table 3	1	15	8
12	Baumgaertner et al. (2002)	9	German	reading	sentences	lexical decision	anomaly	anomalous > expected	Table 3	1	1	6
13	Bedny et al. (2008)	16	American English	reading	word pairs	relatedness judgment	other	relatedness	Table 2	1	4	8
14	Chan et al. (2004)	8	Mandarin Chinese	reading	words	covert word generation	ambiguity	ambiguous > unambiguous	Table 1	1	17	*
15	Copland (2003)	12	Australian English	reading	word pairs	lexical decision	relatedness	unrelated > related	Table I	1	2	8
16	Giesbrecht et al.	10	American	reading	word	relatedness	relatedness	unrelated > related	Table	1	8	8

	(2004)		English		pairs	judgment			1			
17	Hargreaves et al. (2011)	20	Canadian English	reading	words	semantic categorization	ambiguity	ambiguous > unambiguous	Table 3	1	2	6
18	Hoenig & Scheef (2009)	22	German	reading	sentences	context-verification	ambiguity	ambiguous > unambiguous	Table 2	1	15	8
19	Jenkins & Mitchell (2010)	15	American English	reading	sentences	semantic decision	ambiguity	ambiguous > unambiguous	Table 3	1	1	8
20	Kambara et al. (2013)	38	Japanese	reading	sentences	naturalness decision task	anomaly	anomalous > non-anomalous	Table 2	1	4	8
21	Kiehl et al. (2002)	28	American English	reading	sentences	semantic decision	anomaly	incongruent end word > congruent end word	Table 1	1	12	8
22	Mason & Just (2007)	12	American English	reading	sentences	semantic decision	ambiguity	ambiguous > unambiguous	Table 1	1	6	8
23	Nieuwland et al. (2012)	20	Basque	reading	sentences	acceptability judgment	anomaly	anomalous > non-anomalous	Table II	1	12	10
24	Snijders et al. (2009)	28	Dutch	reading	sentences	passive reading	ambiguity	ambiguous > unambiguous	Table 5	1	12	10
25	Wheatley et al. (2005)	18	American English	reading	word pairs	read aloud second word in word pair	relatedness	unrelated > related	Table 1	1	13	4.5
26	Whitney et al. (2009)	15	German	reading	word triplets	relatedness judgment	ambiguity	ambiguous > unambiguous	Table 4	1	8	10

								targets				
Syntax												
1	Friederici et al. (2010)	17	German	auditory	sentences	passive listening	anomaly	grammatically incorrect > correct	Table I	1	5	8
2	Herrmann et al. (2012)	25	German	auditory	word pairs	grammaticality judgment	anomaly	grammatically incorrect > grammatically correct	Table II	1	7	3
3	Mack et al. (2013)	27	American English	auditory	sentences	sentence-picture matching	complexity	passive > active	Table 1	1	6	9
4	Meltzer et al. (2009)	24	American English	auditory	sentences	sentence-picture matching	complexity	main effect of syntactic complexity	Table 3	1	1	8
5	Meyer et al. (2012)	22	German	auditory	sentences	respond to visual probe after 16.7% of sentences	complexity	object-first > subject-first	Table 1	1	1	8
6	Obleser et al. (2011) (Exp 1)	16	German	auditory	sentences	sentence matching	complexity	correlation with increasingly complex syntactic structure	Table 1	1	5	8
7	Obleser et al. (2011)	14	German	auditory	sentences	passive	complexity	correlation with	Table	2	1	8

	(Exp 2)					listening		increasingly complex syntactic structure	2			
8	Peelle et al. (2004)	8	American English	auditory	sentences	gender decision	complexity	object-relative > subject-relative	Table 1	1		8
9	Segaert et al. (2011)	24	Dutch	auditory	sentences	actor decision	cross modal priming	no syntax repetition > syntax repetition	Table 1	1	7	8
10	Shetreet & Friedmann (2014)	22	Hebrew	auditory	sentences	semantic decision	complexity	object-first > subject-first WH-movement > canonical	Table 2	1	6	8
11	Tyler et al. (2011)	15	British English	auditory	sentences	passive listening	ambiguity	ambiguous > unambiguous	Table 3	1	3	10
12	Wilson et al. (2014)	24	American English	auditory	sentences	sentence-picture matching	complexity	correlation with increasingly complex syntactic structure	Table 3	1	7	8
13	Bahlmann et al. (2007)	12	German	reading	sentences	passive reading with post-task	complexity	non-canonical > canonical	Table I	1	2	8
14	Bonhage et al. (2014)	18	German	reading	sentence fragments	word order decision	complexity	encoding task: ungrammatical > grammatical	Table 2	1	4	8

15	Bornkessel-Schlesewsky et al.(2009)	30	German	reading	sentences	grammaticality judgment	complexity	object-subject > subject-object	Table 2	1	7	5.65
16	Fiebach et al. (2005)	14	German	reading	sentences	semantic verification of post-sentence probe	complexity	long object > short object	Table II	1	8	6
17	Friederici et al. (2006)	13	German	reading	sentences	grammaticality judgment	anomaly	incorrect > correct	Table 2	1	4	5.6
18	Grewe et al. (2005)	16	German	reading	sentences	acceptability judgment	complexity	permuted non-pronominal n-os > non-permuted non-pronominal n-so	Table II	1	7	5.65
19	Haller et al. (2007)	16	German	reading	sentences	semantic and antonym decision	complexity	more complex > medium complex	Table 2	1	10	8
20	Kambara et al. (2013)	38	Japanese	reading	sentences	naturalness decision	anomaly	syntactically anomalous > non-anomalous	Table 2	1	4	8
21	Lee & Newman (2010)	18	American English	reading	sentences	judge semantic relatedness of post-sentence probe	complexity	more complex syntax > less complex syntax	Table II	1	12	*

22	Makuuchi et al. (2012)	21	German	reading	sentences	respond to visual probe after 20% of stimulus sentences	complexity	linear effect of syntactic movement distance	Table 2	1	6	6
23	McMillan et al. (2012)	16	American English	reading	sentences	syntactic decision	complexity	more complex syntax > less complex syntax	Table 1	1	4	8
24	Newman, et al. (2010)	20	American English	reading	sentences	semantic relatedness of post-stimulus probe decision	complexity	more complex syntax > less complex syntax	Table 1	1	3	8
25	Nieuwland et al. (2007)	20	Dutch	reading	sentences	passive reading	ambiguity	referential ambiguity > no ambiguity	Table 2	1	8	10
26	Nieuwland et al. (2012)	20	Basque	reading	sentences	acceptability judgment	complexity	more complex syntax > less complex syntax	Table II	1	12	10
27	Novais-Santos et al. (2007)	20	American English	reading	sentences	passive reading	ambiguity	less consistent > more consistent	Table 4	1	2	*
28	Quiñones et al. (2014)	21	Spanish	reading	sentences	grammaticality judgment	complexity	person mismatch > unagreement	Table 3	1	10	8

Table II

Table II. Clusters for the main ALE analysis with all 54 studies, including number of contributing foci ([]), reported at pID $q < 0.001$, with a cluster threshold of 200mm^3 . IFG: Inferior Frontal Gyrus; IPL: Inferior Parietal Lobule; ITG: Inferior Temporal Gyrus; MTG: Middle Temporal Gyrus; PG: Precentral Gyrus; POp: pars orbicularis; POrb: pars orbitalis; PTr: pars triangularis; STG: Superior Temporal Gyrus. Probabilities are included for Brodmann Areas (BA) 44 and 45 when available.

Cluster	mm ³	ALE value	x	y	z	Anatomy	Contributing experiments
1	10608	0.050	-50	14	18	Left POp (probability BA44 43%)	Bedny et al. (2008) [1] Newman et al. (2010) [1] Bornkessel et al. (2009) [3] Novais-Santos et al. (2007) [1]
		0.029	-38	4	32	Left PG (probability BA44 16%)	Fiebach et al. (2005) [2] Obleser & Kotz (2010) [1] Friederici et al. (2010) [1] Obleser et al. (2011) Exp1 [2]
		0.025	-44	26	14	Left PTr (probability BA45 17%)	Grewe et al. (2005) [3] Obleser et al. (2011) Exp2 [1] Haller et al. (2007) [1] Quinones et al. (2014) [1]
		0.020	-32	20	10	Left PTr	Han et al. (2007) [1] Rissmann et al. (2003) [1]
		0.018	-48	6	30	Left PG (probability BA44 25%)	Hargreaves et al. (2011) [2] Rodd et al. (2005) [3] Herrmann et al. (2012) [1] Rodd et al. (2010) [1]
		0.018	-44	18	34	Left POp	Kiehl et al. 2002) [2] Ruff et al. (2008) [1] Kotz et al. (2002) [2] Segaert et al. (2011) [1] Mack et al. (2013) [1] Tesink et al. (2009) [5] Makuuchi et al. (2012) [2] Tyler et al. (2011) [1] McMillan et al. (2012) [1] Whitney et al. (2009) [2]

							Meltzer et al. (2010) [1] Meyer et al. (2012) [1]	Wilson et al. (2014) [1]
2	3648	0.023	-56	-28	0	Left MTG	Fiebach et al. (2005) [2]	Rissmann et al. (2003) [1]
		0.023	-58	-38	4	Left MTG	Friederici et al. (2010) [2]	Rodd et al. (2005) [1]
		0.023	-58	-32	2	Left MTG	Haller et al. (2007) [1]	Ruff et al. (2008) [1]
		0.022	-58	-8	0	Left STG	Han et al. (2007) [1]	Shetreet et al. (2013) [1]
		0.022	-52	-48	4	Left MTG	Herrmann et al. (2012) [1] Lee & Newman (2010) [1] Newman et al. (2010) [1] Obleser & Kotz (2010) [1]	Tesink et al. (2009) [3] Wheatley et al. (2005) [2] Wilson et al. (2014) [1]
3	776	0.019	42	18	14	Right POp	Chan et al. (2004) [1]	Grewe et al. (2005) [1]
		0.015	40	22	22	Right PTr	Fiebach et al. (2005) [1]	Snijders et al. (2009) [1]
		0.014	44	16	30	Right POp		
4	768	0.019	6	-66	44	Right Precuneus	Kambara et al. (syntax) (2013) [1]	Nieuwland et al. (2007) [1]
		0.017	-2	-68	46	Left Precuneus	Lee & Newman (2010) [1] Makuuchi et al. (2012) [1]	Nieuwland et al. (syntax) (2010) [2] Quiñones et al. (2014) [1]
5	736	0.022	44	-22	6	<i>No area assigned</i>	Friederici et al. (2010) [1]	Kuperberg et al. (2000) [1]

							Herrmann et al. (2012) [1]	Ruff et al. (2008) [1]
6	536	0.021	26	20	10	<i>No area assigned</i>	Bornkessel et al. (2009) [1] Mason & Just 2007) [1]	Ruff et al. (2008) [1]
7	536	0.026	-38	0	56	Left PG	Lee & Newman (2010) [1] Mack et al. (2013 [1]	Tesink et al. (2009) [1] Wilson et al. (2014) [1]
8	376	0.019	-32	-56	38	Left IPL	Bornkessel et al. (2009) [1]	Lee & Newman (2010) [1]
9	248	0.019	-52	-50	-10	Left ITG	Rodd et al. (2005) [1]	Snijders et al. (2009) [1]
10	232	0.017	-46	28	-4	Left POrb	Lee & Newman (2010) [1]	Whitney et al. (2009) [1]

Table III

Table III. Activated clusters for the analysis on the studies grouped by the factors ‘Semantics’, ‘Syntax’, reported at $pID < 0.001$, with a cluster threshold of 200mm^3 . Coordinates given in MNI space, including number of contributing foci ‘[]’. IFG: Inferior Frontal Gyrus; MTG: Middle Temporal Gyrus; PG: Precentral Gyrus, POP: pars orbicularis; POrb: Pars Orbitalis; PTr: pars triangularis; SMA: Supplementary Motor Area, SMG: Supramarginal Gyrus; STG: Superior Temporal Gyrus. Probabilities are included for Brodmann Areas (BA) 44 and 45.

Cluster	mm ³	ALE value	x	y	z	Anatomy	Contributing studies
Semantics							
1	4056	0.025	-52	16	20	Left IFG (POp, probability BA44: 22%, BA45: 11%)	Bedny et al. (2008) [1] Rissmann et al. (2003) [1] Han et al. (2007) [1] Rodd et al. (2005) [3]
		0.020	-46	28	12	Left IFG (PTr, probability BA45: 19%)	Hargreaves et al. (2011) [1] Rodd et al. (2010) [1] Kiehl et al. (2002) [2] Ruff et al. (2008) [1]
		0.015	-46	16	32	Left IFG (POp, probability BA44: 21%, BA45: 9%)	Kotz et al. (2002) [1] Tesink et al. (2009) [5] Obleser & Kotz (2010) [1] Whitney et al. (2009) [2]
2	816	0.019	-58	-8	0	Left STG	Rissmann et al. (2003) [1] Ruff et al. (2008) [1] Rodd et al. (2005) [1] Wheatley et al. (2005) [2]
3	496	0.019	-52	-50	-10	Left ITG	Kiehl et al. (2002) [1] Snijders et al. (2009) [1] Rodd et al. (2005) [1]
4	256	0.015	24	22	10	<i>No area assigned</i>	Kotz et al. (2002) [1] Ruff et al. (2008) [1]
5	208	0.014	-36	0	26	<i>No area assigned</i>	Hargreaves et al. (2011) [1] Kotz et al. (2002) [1]
6	200	0.013	-32	30	-12	Left POrb	Kambara et al. (2013) [1] Kiehl et al. (2002) [1]
Syntax							
1	4144	0.035	-50	12	16	Left IFG (POp, probability	Bornkessel et al. (2009) [2] Meltzer et al. (2010) [1]

						BA44: 52%	Fiebach et al. (2005) [1]	Obleser et al. (2011) Exp1 [2]
		0.016	-32	20	8	Left Insula	Grewe et al. (2005) [2]	Obleser et al. (2011) Exp2 [1]
							Herrmann et al. (2012) [1]	Segaert et al. (2011) [1]
							Makuuchi et al. (2012) [1]	Tyler et al. (2011) [1]
							Meyer et al. (2012) [1]	Wilson et al. (2014) [1]
2	1368	0.019	6	-66	44	Right Precuneus	Kambara et al. (2013) [1]	Nieuwland et al. (2007) [1]
		0.017	-2	-68	46	Left Precuneus	Lee & Newman (2007) [1]	Nieuwland et al. (2010) [2]
							Makuuchi et al. (2012) [1]	Quinones et al. (2014) [1]
3	1336	0.019	-54	-26	0	Left MTG	Fiebach et al. (2005) [1]	Lee & Newman (2010) [1]
		0.017	-60	-36	2	Left MTG	Friederici et al. (2010) [1]	Newman et al. (2010) [1]
		0.011	-52	-48	4	Left MTG	Herrmann et al. (2012) [1]	Shetreet et al. (2013) [1]
4	1064	0.026	-38	4	34	Left PG	Bornkessel et al. (2009) [1]	Mack et al. (2013) [1]
							Grewe et al. (2005) [1]	Makuuchi et al. (2012) [1]
5	544	0.018	-30	-56	38	Left IPL	Bornkessel et al. (2009) [1]	Tyler et al. (2011) [1]
							Lee & Newman (2010) [1]	
6	448	0.017	-2	14	54	Left SMA	Segaert et al. (2011) [1]	Wilson et al. (2014) [1]
7	416	0.019	-38	0	56	Left PG	Lee & Newman (2010) [1]	Wilson et al. (2014) [1]
							Mack et al. (2013) [1]	
8	200	0.016	-60	-34	38	Left SMG	Kambara et al. (2013) [1]	Nieuwland et al. (2010) [1]

Table IV

Table IV. Results for the subtraction analyses contrasting semantic and syntactic processing, including number of contributing foci ([]), reported at $p < 0.05$, with a cluster threshold of 200mm^3 . FFG: Fusiform Gyrus; IFG: Inferior Frontal Gyrus; IPL: Inferior Parietal Lobule; ITG: Inferior Temporal Gyrus; MOG: Middle Occipital Gyrus; PG: Precentral Gyrus; POp: pars orbicularis; POrb: pars orbitalis; PTr: pars triangularis; SFG: Superior Frontal Gyrus, SMedG: Superior Medial Gyrus, SMG: Supramarginal Gyrus; SOG: Superior Occipital Gyrus. Clusters that did not list a minimum of two experiments are displayed in *italics*.

Cluster #	mm ³	Z	x	y	z	Anatomy	Contributing experiments
Semantics > Syntax							
1	2992	2.69	-44	-50	-14	Left ITG	Bekinschtein et al. (2011) [1]
		2.57	-52	-54	-14	Left ITG	Kiehl et al. (2002) [3]
		2.54	-44	-50	-10	Left ITG	Rodd et al (2005) [1]
		2.53	-50	-50	-18	Left ITG	
		2.40	-46	-50	-22	Left ITG	
		2.31	-42	-42	-20	Left FFG	
		2.25	-46	-44	-20	Left ITG	
		2.18	-47	-59	-20	Left FFG	
		2.17	-50	-40	-21	Left ITG	
		2.02	-45	-39	-24	Left ITG	
		1.84	-44	-28	-22	Left ITG	

		1.82	-48	-34	-24	Left ITG	
2	1008	2.76	35	8	-12	<i>No area assigned</i>	Kiehl et al. (2002) [1] Nieuwland et al (2010) [1]
		2.07	32	16	-20	Right Insula	
		1.84	30	16	-6	<i>No area assigned</i>	
3	968	2.04	-18	54	18	Left SFG	Kambara et al. (2013) [1] Mason & Lee (2007) [1]
4	904	2.25	-8	50	38	<i>Left SMedG</i>	<i>Hoening & Scheef (2009) [1]</i>
		2.22	-6	42	47	<i>Left SMedG</i>	
		2.17	-7	45	43	<i>Left SMedG</i>	
		1.96	-2	48	40	<i>Left SMedG</i>	
		1.79	-14	34	40	<i>Left SFgG</i>	
5	592	2.51	-28	38	-14	<i>Left MOG</i>	-
		1.99	-38	30	-17	<i>Left IFG (POrb_</i>	
6	528	2.15	-56	-12	-4	<i>Left STG</i>	-
		1.91	-50	-10	-6	<i>Left STG</i>	
		1.90	-60	-8	0	<i>Left STG</i>	
		1.79	-64	-6	2	<i>Left STG</i>	

7	488	2.18	-52	26	16	Left IFG (PTr, probability BA45: 46%)	Tesink et al (2009) [1]
		1.88	-50	36	12	Left IFG (PTr, probability BA45: 40%)	
		1.84	-50	33	14	Left IFG (PTr, probability BA45: 65%)	
8	384	2.17	-48	18	30	Left IFG (PTr, probability BA45: 14%, BA44: 11%)	Tesink et al (2009) [1]
		2.10	-54	18	32	Left IFG (PTr, probability BA45: 32%, BA44: 22%)	
9	376	2.47	-11	53	31	Left SFG	Chan et al. (2004) [1]
		2.24	-10	48	24	Left SFG	Nieuwland et al. (2012) [1]
Syntax > Semantics							
1	4280	3.43	-13	-64	47	Left SPL	Kambara et al. (2013) [1]
		3.01	-21	-65	48	Left SPL	Lee & Mason (2010) [1]
		2.74	-8	-72	44	Left Precuneus	Makuuchi et al. (2012) [1]
		2.40	-2	-66	48	Right Precuneus	Nieuwland et al. (2007) [2]
		2.38	10	-66	43	Right Precuneus	Nieuwland et al. (2010) [2]

		2.12	4	-74	40	Right Precuneus	Quinones et al. (2014) [1] Wilson et al. (2014) [1]
2	1344	2.91	-24	-58	38	Left MOG	Bornkessel et al. (2009) [1] Lee & Mason (2010) [1] Makuuchi et al. (2012) [1] Tyler et al. (2011) [1]
		2.19	-28	-58	44	Left SPL	
		2.13	-28	-52	34	Left AG	
		2.08	-32	-48	34	<i>No area assigned</i>	
		1.85	-31	-52	42	Left IPL	
3	1200	2.56	4	12	52	Left SMedG	Haller et al. (2007) [1] Lee & Mason (2010) [1] Wilson et al. (2014) [1]
		2.13	8	14	50	Left SMedG	
		2.13	6	16	54	Left SMedG	
		1.98	-2	-2	54	Left SMedG	
4	1016	2.38	-34	20	0	Left Insula	Meltzer et al. (2010) [1] Tyler et al. (2011) [1]
		2.26	-38	14	10	Left Insula	
		2.24	-38	22	0	Left Insula	
		2.11	-40	12	16	Left IFG (POp)	
		2.05	-48	10	14	Left IFG (POp, probability BA44: 17%)	
5	664	2.23	-42	1	36	Left PG	<i>Grewe et al (2005) [1]</i>

		1.90	-32	2	38	Left PG	
6	552	2.24	50	-44	44	Right SMG	Friederici et al. (2006) [1]
		2.08	47	-43	40	Right IPL	Nieuwland et al. (2010) [1]
		2.05	44	-46	45	Right IPL	
7	416	2.72	-24	-68	34	<i>Left SOG</i>	<i>Bonhage et al. (2014) [1]</i>
		2.66	-20	-67	34	<i>Left SOG</i>	

Table V. Results for the subtraction analyses contrasting semantic and syntactic processing without the 10 studies using an anomaly manipulation, reported at $p < 0.05$, with a cluster threshold of 200mm^3 , including number of contributing foci ([]). ACC: Anterior Cingulate Cortex; HG: Heschl's Gyrus; FFG: Fusiform Gyrus; IFG: Inferior Frontal Gyrus; IPL: Inferior Parietal Lobule; ITG: Inferior Temporal Gyrus; MOG: Middle Occipital Gyrus; PG: Precentral Gyrus; POp: Pars Opercularis; RO: Rolandic Operculum; SOG: Superior Occipital Gyrus; SMedG: Superior Medial Gyrus; STG: Superior Temporal Gyrus. Clusters that did not list a minimum of two experiments are displayed in *italics*.

Cluster	mm^3	Z	x	y	z	Anatomy	Contributing studies
Semantics > Syntax							
1	2072	2.64	-54	-14	-2	Left STG	Rissmann et al. (2003) [1]
		2.62	-58	-14	-6	Left MTG	Ruff et al. (2008) [1]
		2.61	-42	-14	2	Left Insula	Wheatley et al. (2005) [1]
		2.45	-58	-14	2	Left STG	
		2.16	-47	-12	0	Left STG	
		2.16	-52	-12	6	Left HG	
		2.14	-56	-12	6	Left HG	
		1.78	-58	-8	8	Left RO	
2	976	2.49	-45	-49	-18	Left ITG	Bekinschtein et al. (2011) [1]
		2.43	-52	-54	-14	Left ITG	Rodd et al. (2005) [1]
		2.27	-44	-48	-24	Left FFG	

		2.15	-44	-44	-20	Left FFG	
		2.07	-45	-53	-8	Left ITG	
3	384	1.99	1	29	0	Left ACC	-
		1.78	0	28	-4	Right ACC	
		1.77	4	21	0	No area given	
		1.75	8	18	-2	Right Caudate Nucleus	
		1.74	6	25	1	No area given	
		1.70	6	34	-3	Right ACC	
4	304	2.60	10	16	10	Right Caudate Nucleus	Mason & Just (2004) [1]
5	240	2.00	-7	45	42	Left SMedG	-
		1.99	-9	49	37	Left SMedG	
		1.95	-10	44	38	Left SMedG	
Syntax > Semantics							
1	3832	2.91	-17	-64	47	Left SPL	Lee et al. 2010 [1]
		2.62	-18	-68	50	Left SPL	Makuuchi et al. (2012) [1]
		2.37	-8	-72	46	Left Precuneus	Nieuwland et al. (2007) [2]
		2.12	-2	-66	48	Left Precuneus	Nieuwland et al. (2010) [2]
		1.80	8	-68	41	Right Precuneus	Quinones et al. (2014) [1] Wilson et al. (2014) [1]

2	1112	2.93	-24	-58	38	<i>Left MOG</i>	<i>Lee & Mason (2004) [1]</i>
		2.66	-26	-60	42	<i>Left IPL</i>	
		2.01	-28	-52	34	<i>Left AG</i>	
		1.95	-32	-48	34	<i>No area given</i>	
		1.77	-30	-52	42	<i>Left IPL</i>	
3	840	2.36	-42	10	18	Left IFG (POp, probability for BA44: 3%)	Meltzer et al. (2010) [1] Obleser et al. (2011) (Exp2) [1] Tyler et al. (2011) [1]
		2.11	-38	14	10	Left Insula	
4	760	2.38	4	12	52	<i>Left SMedG</i>	<i>Lee & Mason (2004) [1]</i>
		2.18	-2	10	50	<i>Left SMedG</i>	
		1.99	8	14	50	<i>Right SMedG</i>	
5	592	2.12	-42	0	36	<i>Left PG</i>	<i>Grewe et al. (2005) [1]</i>
		1.94	-36	-2	42	<i>Left PG</i>	
		1.81	-32	2	36	<i>Left PG</i>	
6	488	2.06	-58	-32	4	<i>No area given</i>	-
		1.88	-54	-34	0	<i>Left MTG</i>	
		1.75	-59	-30	-3	<i>Left MTG</i>	

7	400	2.67	-24	-68	34	<i>Left SOG</i>	<i>Bonhage et al. (2014) [1]</i>
		2.60	-20	-67	34	<i>Left SOG</i>	
8	368	1.99	-40	-4	50	Left PG	Lee et al. (2010) [1] Mack et al. (2013) [1]
9	320	2.36	-34	20	0	<i>Left Insula</i>	-

Figure 1
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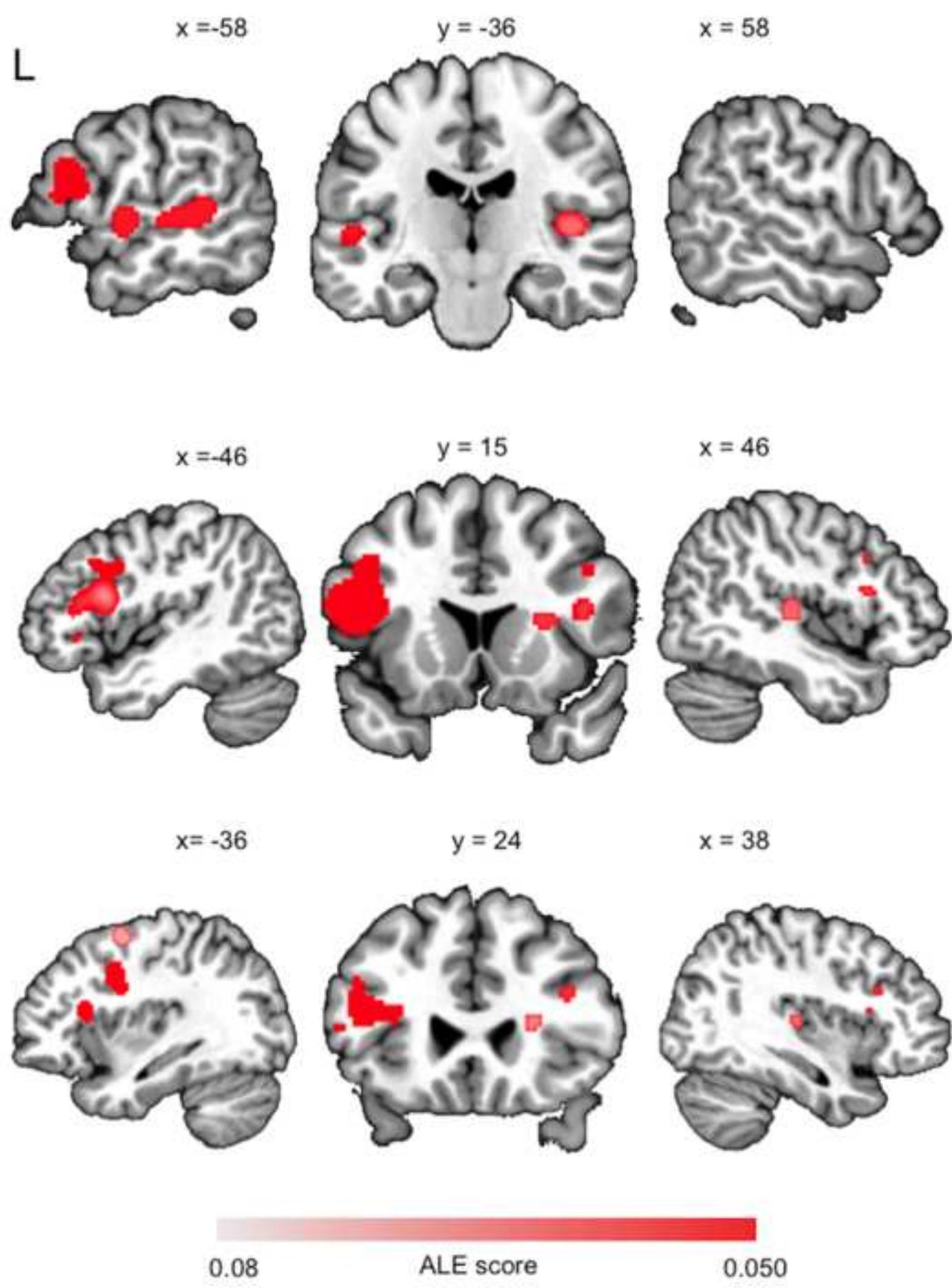


Figure 2
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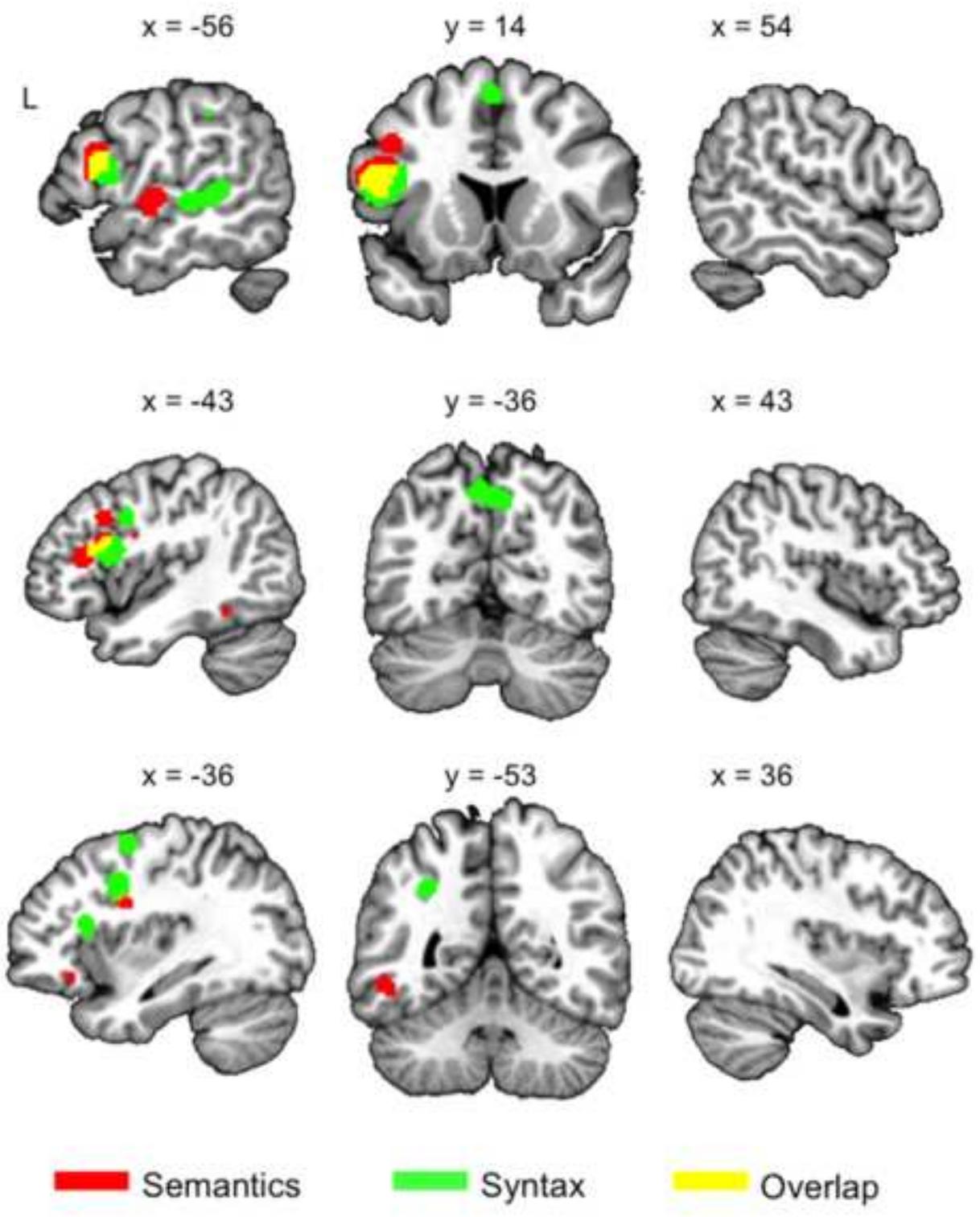


Figure 3
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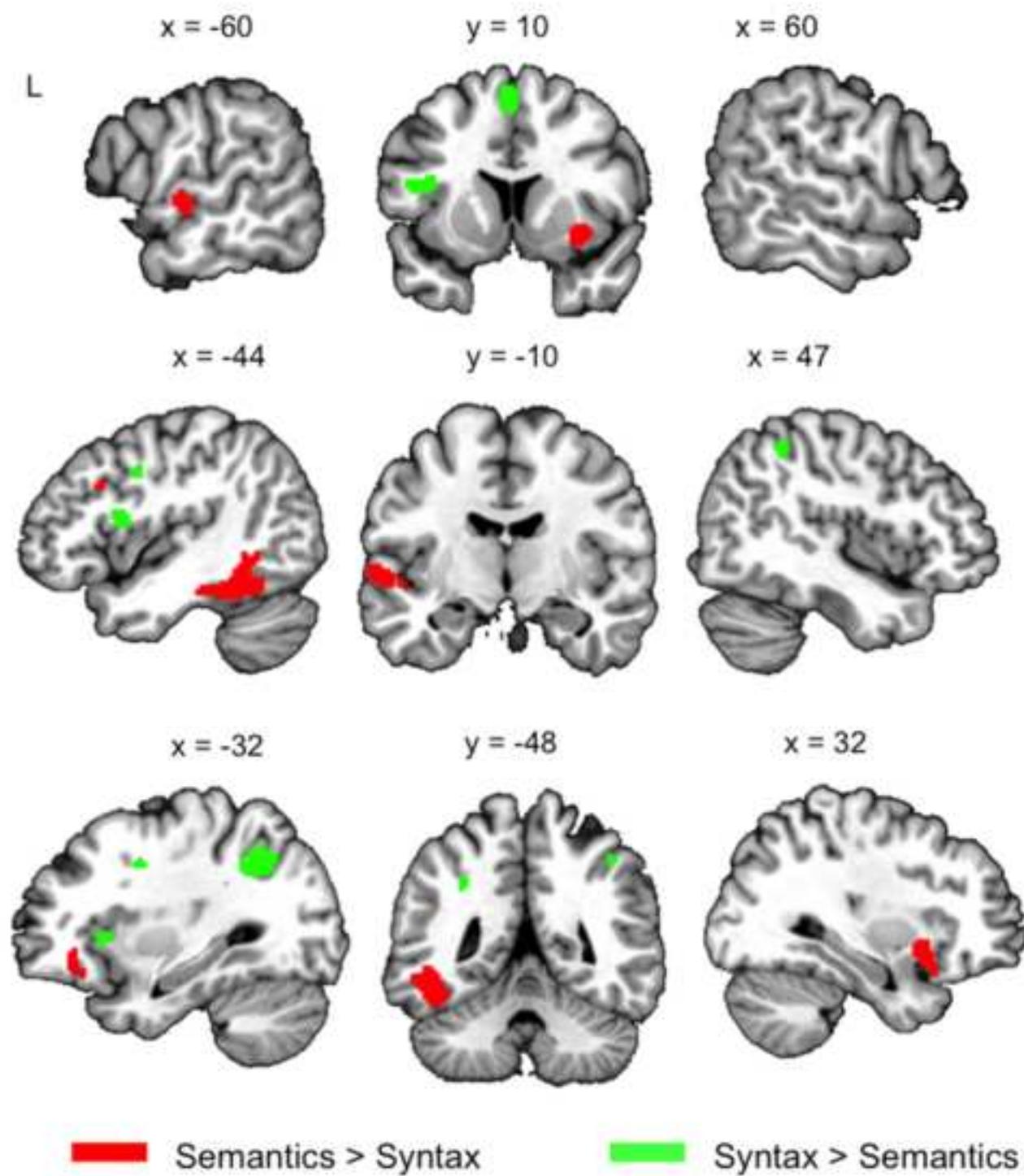


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