Neuroanatomical dissociations of syntax and semantics revealed by lesion-symptom mapping

Short title: neuroanatomical dissociations of syntax and semantics

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Abstract

In the early and mid 1800s, scientists debated whether the human brain was functionally differentiated with respect to cognition. The issue was largely resolved when specific language impairments were identified following focal patterns of brain damage. However, neuroimaging has revived this discussion, as many studies find similar syntactic and semantic effects across the set of brain regions implicated in language. Here we address this modern debate using lesion-symptom mapping in two large, partially-overlapping groups of people with left hemisphere brain damage due to stroke (N=121, N=92). We identified multiple measure by region interaction effects, associating damage to the posterior middle temporal gyrus with syntactic comprehension deficits, damage to posterior inferior frontal gyrus with expressive agrammatism, and damage to inferior angular gyrus with semantic category word fluency deficits. Our results are inconsistent with recent hypotheses that regions of the language network play similar roles in high-level linguistic processing.

Introduction

At its core, language consists of pairings of form and meaning. Linguistic form at the sentence level consists of syntactic structure: sequences of words and their hierarchical arrangement. Linguistic meaning consists of concepts denoted by words and the interpretation of their combination. These domains are further subdivided into distinct types, such as the distinction between hierarchical and linear syntax (Berwick & Chomsky, 2016; Matchin & Hickok, 2020)

and between taxonomic and thematic features (Binder & Desai, 2011; Estes et al., 2011; Lin & Murphy, 2001; Schwartz et al., 2011). Despite this differentiation, neuroimaging experiments typically find that contrasts of syntax and semantics highly overlap in a set of perisylvian brain regions in association cortex (Diachek et al., 2020; Fedorenko, Nieto-Castañon, et al., 2012; Fedorenko et al., 2020; Humphries et al., 2006, 2007; Matchin et al., 2017, 2019). In response to this, some researchers have suggested that higher-level linguistic processing is distributed throughout language-related cortex, and that individual brain regions are not differentiated with respect to syntactic and semantic function (Blank et al., 2016, p. 201; Fedorenko et al., 2020; Fedorenko, Nieto-Castañón, et al., 2012; Fedorenko & Blank, 2020; Mollica et al., 2020). However, while syntax and semantics are two separate aspects of language, they are systematically connected: inverting the order of words in a sentence like *dog bites man* results in a far more surprising meaning than the original. Thus, any experimental manipulation of syntax is likely to affect semantic interpretation, and vice versa. This tight connection poses a serious obstacle to identifying the potentially distinct brain bases of higher-level linguistic functions through the use of neuroimaging experiments.

Lesion-symptom mapping can help resolve this conundrum by identifying brain regions causally involved in linguistic functions (Bates et al., 2003; Wilson, 2017). Previous lesion-symptom mapping studies have associated different language-related brain regions with different syntactic and semantic processes (Ding et al., 2020; Dronkers et al., 2004; Gleichgerrcht et al., 2016; Kristinsson et al., 2020; Magnusdottir et al., 2013; Matchin et al., 2020; Mesulam et al., 2015; Pillay et al., 2017; Riccardi et al., 2020; Rogalsky et al., 2018; Schwartz et al., 2011; Thothathiri et al., 2012; Wilson, Dronkers, et al., 2010; Wilson, Henry, et al., 2010). However, few studies report task by region interaction effects which would provide strong evidence for functional dissociations across regions. Guided by a recent theoretical model of syntax and semantics in the brain (Matchin & Hickok, 2020), we assessed three measures tapping into distinct linguistic processes: syntactic comprehension, expressive agrammatism, and semantic category word fluency, in a lesion-symptom mapping study with two partially overlapping cohorts of people with chronic left hemisphere damage following stroke (N = 121 and N=92). We hypothesized that we would find significant measure by region interaction effects, supporting selectivity for distinct higher-level linguistic processes in different brain regions.

Materials & Methods

Subjects & Measures

In two, partially overlapping groups of subjects, we assessed three different measures tapping into different aspects of syntax and semantics: (i) syntactic comprehension (Group 1, N=121), (ii) expressive agrammatism (Group 2, N=92), and (iii) semantic category word fluency (Group 2, N=92). Subjects were assessed on a number of language batteries which were part of multiple studies on aphasia recovery, which were not designed for the analyses that we report here. Group 1 subjects were the same as reported in den Ouden et al. (2019) and Kristinsson et al. (2020). 47 subjects were included solely in den Ouden et al. (2019), 48 subjects were included solely in Kristinsson et al. (2020), and 26 subjects were included in both studies. Group 2 subjects were the same as reported in den Ouden et al., (2019, N = 39) and Matchin et al., (2020, N = 53). All of the lesion maps and behavioral data for subjects enrolled in this study are available for

download at https://www.dropbox.com/sh/3w4aeizgypfs7sd/AAB-W8Yn5qDUFeBj90WKsBqAa?dl=0.

The *syntactic comprehension* measure was derived from two different sentence-picture matching tasks reported in more detail elsewhere (den Ouden et al., 2019; Kristinsson et al., 2020). The tasks involved a range of constructions, but our focus here is on complex, semantically reversible sentences with non-canonical word order. These included object-extracted clefts (Kristinsson et al., 2020; e.g., *it is the boy that chases the cat*), object-extracted relative clauses (den Ouden et al., 2019; e.g., *the boy that the girl chased is happy*), and object-extracted Wh-questions (both studies; e.g. *which boy did the girl chase?*). Sentences of this sort have a long history in research on syntactic ability in comprehension because (i) lacking canonical English subject-verb-object word order and (ii) lacking semantic plausibility constraints (c.f., *which apple did the boy eat?*), they require syntactic analysis for determining who is doing what to whom (Caramazza & Zurif, 1976). Performance on such sentences is often compared to comprehension of simple active-voice sentences (i.e., the noun verbed the noun) as a control for speech perception, lexical processing, basic ability to infer an event structured based on a sequence of words, and working memory or decision-making resources involved in performing a sentence-picture matching task. Thus, our syntactic comprehension measure was computed as the average performance on complex sentences with performance on simple, semantically reversible active sentences covaried out using linear regression. For subjects who performed both studies (N = 26), in order to provide the most reliable estimate, scores were averaged across the two studies, which contained the same number of trials (5 trials per sentence type).

The *expressive agrammatism* measure was derived from samples of connected speech production elicited either by (i) describing the Cookie Theft picture (Goodglass & Kaplan, 1983, as reported in den Ouden et al., 2019) or (ii) retelling the story of Cinderella in their own words (MacWhinney et al., 2011, as reported in Matchin et al., 2020). The presence of expressive agrammatism was determined as described in Matchin et al., (2020). Briefly, production samples were rated independently by speech and language experts for the systematic simplification of sentence structure and omission of function words and morphemes. This resulted in a categorical assessment for each subject, either agrammatic or not. We included speech rate as a covariate using logistic regression (words per minute during the task) in order to focus on residual morphosyntactic sequencing abilities rather than general speech production abilities.

The *semantic category word fluency* measure came from the Word Fluency subtest of the Western Aphasia Battery - Revised (Kertesz, 2007), as administered by a licensed speech language pathologist. Subjects were assessed at a variable number of timepoints (mean = 2.02 assessments, SD = 1.07); we averaged their performance across these assessments in order to provide the most reliable estimate. The Word Fluency subtest involves asking the subject to name as many animals as possible within one minute (maximum score is 20). Word fluency roughly assesses two broad categories of abilities: access to conceptual-semantic representations and more general search, selection, and articulatory abilities (Chertkow & Bub, 1990; Troyer et al., 1997; Unsworth et al., 2011). Notably, a previous lesion-symptom mapping study by Baldo et al. (2006) found that deficits in the same Word Fluency task were associated with temporal and inferior parietal damage, whereas letter fluency was associated with frontal and anterior parietal damage (see Libon et al., 2009 for similar findings). This suggests that Word Fluency

may be less impacted by non-linguistic mechanisms than other fluency measures, consistent with the fact that patients with semantic dementia perform worse on semantic category fluency measures than letter fluency relative to patients with Alzheimer's disease (Marczinski & Kertesz, 2006). Regardless, to focus our measure more neatly on conceptual-semantic access, we incorporated the same speech rate covariate we used for the expressive agrammatism analysis to control for non-semantic factors.

All subjects were recruited through local advertisement. They provided informed consent to participate in this study, which was approved by the Institutional Review Boards at the University of South Carolina and the Medical University of South Carolina. All subjects had at least one ischemic stroke to the left hemisphere at least six months prior to study inclusion and were also pre-morbidly right handed (self- disclosed). Demographic information for the two groups of subjects is shown in Table 1.

	Group 1	**Group 2**
Measures	Syntactic Comprehension	Semantic Category Word Fluency Expressive Agrammatism
Total number of subjects	N = 121	N = 92
Sex	79 male, 42 female	60 male, 32 female
Age (years)	59.6 (SD = 10.6)	58.7 (SD = 11.1)
Months post-stroke at initial testing	47.5 (SD = 52.4)	46.4 (SD = 49.6)
Education (years)	15.4 (SD = 2.3)	15.3 (SD = 2.3)
Lesion Volume (mm^3)	112,652 (SD = 94,945)	96,175 (SD = 84,514)
WAB AQ	66 (SD = 26.9)	75.8 (SD = 19.9)

Table 1. Subject information for the two partially overlapping groups of subjects.

Brain Imaging & Lesion mapping

We acquired anatomical MRIs and performed lesion mapping using the same parameters and procedures as described in Fridriksson et al. (2018). Neuroimaging data were collected at the University of South Carolina and the Medical University of South Carolina. Lesions were demarcated onto each subject's T2 image by an expert technician or an expert neurologist blind to the behavioral data.

Lesion overlap maps for both groups are shown in Figure 1 (a & b). Overall, there was good coverage in perisylvian cortex, including all of the selected regions of interest (described below).

Region of Interest (ROI) definition

To define ROIs for language-related brain regions involved in higher-level linguistic processing, we used the statistical maps associated with a previous fMRI study on sentence processing (Matchin et al., 2017). This study compared multiple conditions, including full natural sentences (e.g., *the poet might recite a verse*) and jabberwocky sentences, which involve the substitution of pseudowords for content words (e.g., *the tevill will sawl a pand*). The contrast of natural sentences > jabberwocky sentences highlighted a number of language-related brain regions in association cortex that are frequently identified in brain imaging studies of syntax and semantics. We therefore used this contrast with a reduced voxel-wise threshold of $p < 0.01$ (Figure 1c). We selected clusters corresponding to six left hemisphere regions that have been previously implicated in higher-level linguistic processing (Figure 1d), including most prominently syntax and semantics: the inferior angular gyrus (iAG), the posterior middle temporal gyrus (pMTG), the anterior superior temporal sulcus (aSTS), the temporal pole (TP), the posterior inferior frontal gyrus (pIFG), and the anterior inferior frontal gyrus (aIFG). These clusters were contiguous at local minima, and so were manually separated at these junctures to form six separate ROIs.

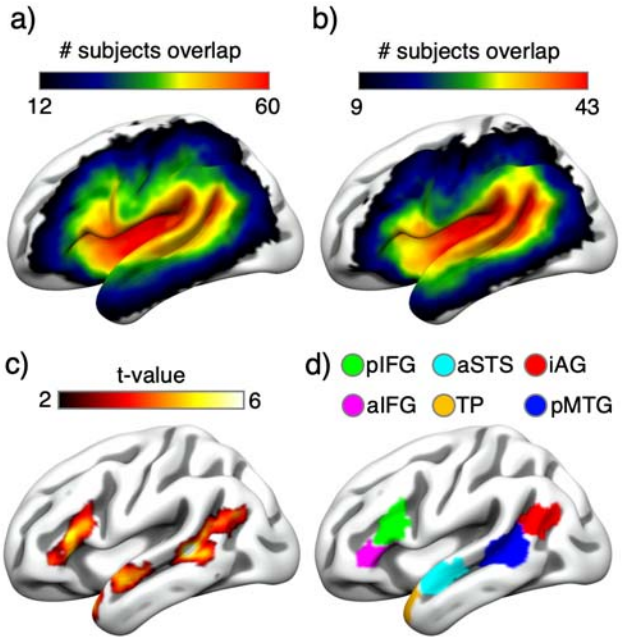

Figure 1. (a) Lesion overlap map for the Group 1 (N = 121), assessed for *syntactic comprehension*. The lower boundary of 12 corresponds to regions where at least 10% of subjects had damage. (b) (a) Lesion overlap map for Group 2 group (N = 92), assessed for *semantic category word fluency* and *expressive agrammatism*. The lower boundary of 9 corresponds to regions where at least 10% of subjects had damage. (c) Statistical contrast of natural sentences > jabberwocky sentences from Matchin et al., (2017) at the uncorrected voxel-wise threshold of $p < 0.01$. (d) Selected ROIs using the clusters derived from the contrast of natural sentences > jabberwocky sentences from Matchin et al., (2017). Red: inferior angular gyrus (iAG); blue: posterior middle temporal gyrus (pMTG); cyan: anterior superior temporal sulcus (aSTS); orange: temporal pole (TP); magenta: anterior inferior frontal gyrus (aIFG); green: posterior inferior frontal gyrus (pIFG).

Lesion Analyses

We performed ROI-based univariate regression analyses using the set of six ROIs and correcting for multiple comparisons using permutation tests (10,000 permutations) in NiiStat (https://www.nitrc.org/projects/niistat/). We performed additional uncorrected whole-hemisphere voxel-based regression analyses in NiiStat in order to ensure that our ROI analyses did not obscure the true lesion distribution associated with the effects. All univariate analyses were performed within regions that contained at least 10% of sample with lesions in that location and incorporated lesion volume as a covariate in both behavioral and brain measures (DeMarco & Turkeltaub, 2018).

We also performed three hypothesis-driven interaction analyses, one for each measure. The neuroanatomical model of Matchin & Hickok (2020) predicts that pMTG is critically involved in hierarchical syntactic processing for both comprehension and production, whereas the pIFG is involved in morpho-syntactic sequencing primarily for production. With respect to *syntactic comprehension*, we tested the interaction between the pMTG and pIFG. We expected that the pMTG would be implicated, but not pIFG. By contrast, with respect to *expressive agrammatism*, we tested the interaction between pMTG and pIFG, with the expectation that this would primarily reveal deficits in morpho-syntactic sequencing abilities in production, hypothesized to be processed by the pIFG (see Matchin & Hickok, 2020 for a review). With respect to *semantic category word fluency*, we tested the interaction between iAG and aSTS, as both have been strongly associated with conceptual-semantic interpretation, but have been hypothesized to house distinct conceptual representations (Binder & Desai, 2011; Matchin & Hickok, 2020; Schwartz et al., 2011). To test these interactions, we first calculated proportion damage to each ROI and adjusted the data using a rationalized arcsine transform (Studebaker, 1985), and then computed residual damage values by covarying out the effect of lesion volume. We then assessed the region by measure interaction effect in linear regression for each of the three measures of interest in SPSS. We corrected for multiple comparisons using a Bonferroni correction with an adjusted alpha threshold of $p < 0.0167$ for each of the three independent comparisons, controlling the total error at $p < 0.05$.

Results & Discussion

ROI results are shown in Figure 2a. For *syntactic comprehension*, two ROIs showed a significant negative association between percent damage and behavioral scores: pMTG ($Z = -3.23$, $p = 0.00087$) and aSTS ($Z = -2.56$, $p = 0.00695$). For *expressive agrammatism*, two ROIs showed a significant positive association between percent damage and behavioral scores: pIFG ($Z = 3.08$, $p = 0.00135$) and aIFG ($Z = 2.54$, $p = 0.00554$). For the regression analysis of *semantic category word fluency*, one ROI showed a significant negative association between percent damage and behavioral scores: iAG ($Z = -3.73$, $p = 0.000096$). Uncorrected analyses using an individual voxel-level threshold of $p < 0.05$ generally support our ROI analyses (Figure 2b), although the strongest localization of *expressive agrammatism* appears to have been in the inferior frontal sulcus (IFS) rather than the IFG itself.

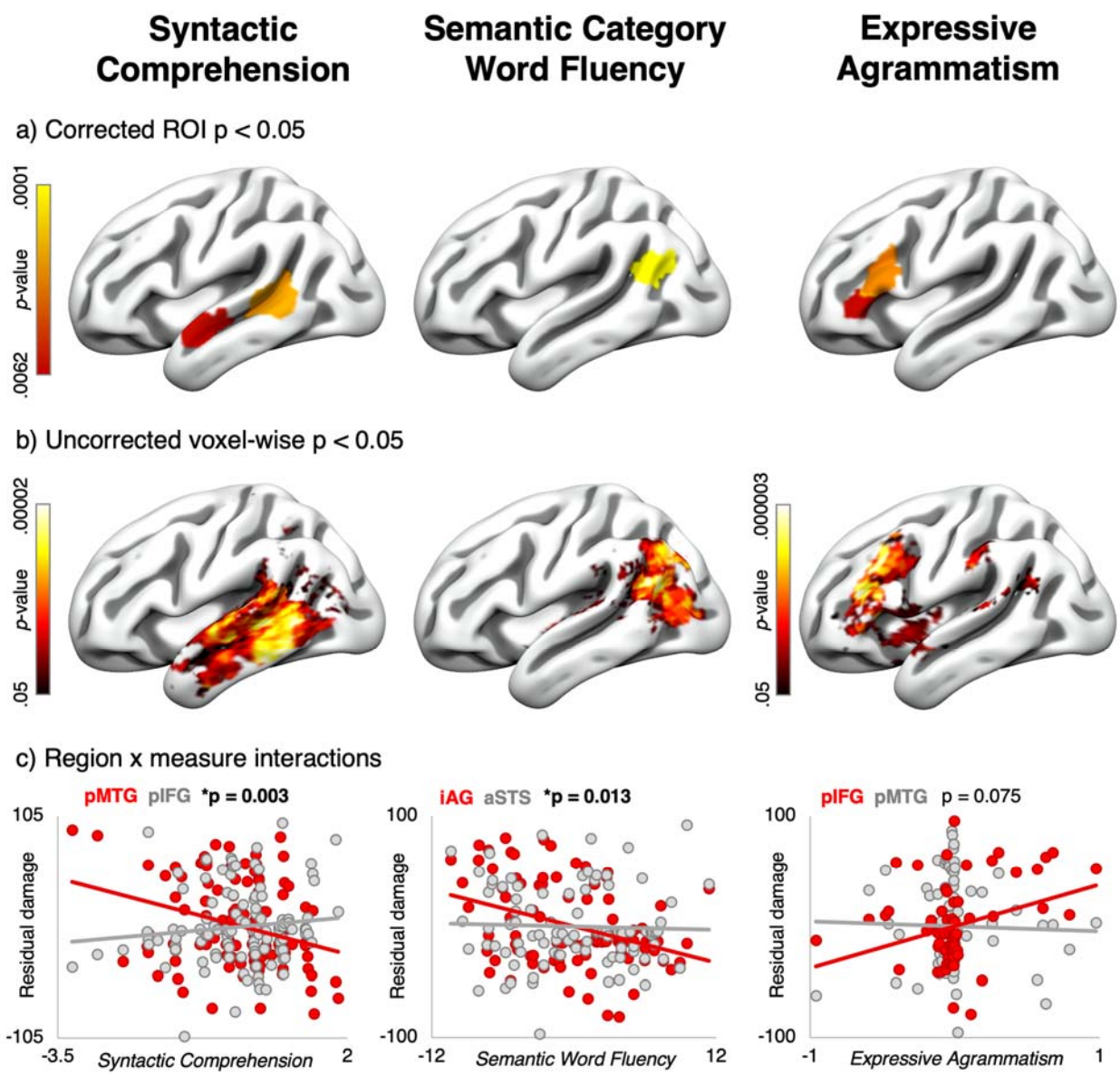

Figure 2. Corrected ROI-based and uncorrected whole-brain analyses for each of the three measures of syntax/semantics. Each measure is identified at top in bold, corresponding to all of the figures underneath. (a) Regression analyses within the selected ROIs, corrected for multiple comparisons using permutation tests ($p < 0.05$). (b) Uncorrected voxel-wise analyses ($p < 0.05$). (c) Scatter plots illustrating three hypothesis-driven *region by measure* interaction analyses, corrected for multiple comparisons using a Bonferroni correction (individual $p < 0.0167$). pMTG = posterior middle temporal gyrus; pIFG = posterior inferior frontal gyrus; iAG = inferior angular gyrus; aSTS = anterior superior temporal sulcus.

Scatterplots illustrating the *region by measure* interactions are shown in Figure 2c. For *syntactic comprehension*, there was a significant interaction between the pMTG and pIFG, such that damage to pMTG was significantly more associated with deficits than the pIFG, $F(1,119) = 9.013$, $p = 0.003$, $\eta^2 = 0.076$. For *expressive agrammatism*, there was nonsignificant interaction between the effects in pMTG and pIFG, such that damage to pIFG was more associated with

agrammatic speech than the pMTG, $F(1,90) = 3.25$, $p = 0.075$, $\eta^2 = 0.036$. For *semantic category word fluency*, there was a significant interaction between the effects in iAG and aSTS, such that damage to iAG was significantly more associated with deficits than the aSTS, $F(1,119) = 6.799$, $p = 0.011$, $\eta^2 = 0.076$.

These results narrow down possible functions of these brain regions with respect to syntax and semantics, and suggest that neuroimaging research critically needs to incorporate insights from lesion symptom mapping in order to understand the architecture of language in the brain. Namely, the *region by measure* interactions we identified present strong challenges to the hypothesis that language-related brain regions underlie a similar function with respect to syntactic or and/or higher-level linguistic processing (Blank et al., 2016; Caplan et al., 1996; Dick et al., 2001; Fedorenko et al., 2020; Fedorenko & Blank, 2020; Mollica et al., 2020).

Our results are much more consistent with neuroanatomical models that posit distinct syntactic and semantic functions to different regions within the language network (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2017; Hagoort, 2014; Matchin & Hickok, 2020; Tyler & Marslen-Wilson, 2008) than with the hypothesis of undifferentiated linguistic function of language-related brain regions. In particular, the model presented by Matchin & Hickok (2020) provides clear explanations for the identified effects and interactions. The model posits that the posterior middle temporal gyrus (pMTG) is critical for processing hierarchical structure for both production and comprehension. Damage to the pMTG was significantly associated with semantic comprehension deficits even when compared to the pIFG. This reinforces previous lesion-symptom mapping studies that have found an association between residual syntactic comprehension scores (regressing out single word comprehension or production) with damage to the posterior temporal lobe (Kristinsson et al., 2020; Pillay et al., 2017; Rogalsky et al., 2018).

Matchin & Hickok suggest that the pIFG is hypothesized to underlie a linear morpho-syntactic system that sequences words and morphemes during speech production, but is not critical for lexical retrieval or syntactic structure building in comprehension. As we have shown previously in subsets of these data (den Ouden et al., 2019; Matchin et al., 2020), and consistent with previous research (Sapolsky et al., 2010; Wilson, Henry, et al., 2010), damage to the pIFG was significantly associated with agrammatic speech deficits, but was not associated with any comprehension deficits. The fact that the voxel-wise analysis identified the main locus of damage with the IFG, and that the interaction between pIFG and pMTG only approached significance, suggests that the role for middle frontal regions in syntax should be further investigated.

The only region significantly associated with deficits in semantic category word fluency was the iAG, similar to a previous study which also identified temporal lobe regions (Baldo et al., 2006). Following previous authors (Binder & Desai, 2011; Mesulam et al., 2015; Schwartz et al., 2011), the Matchin & Hickok model posits that the aSTS the iAG are involved in distinct aspects of conceptual-semantic processing. Namely, the iAG is hypothesized to support relations among concepts, critically encoded by verbs, whereas the aSTS is hypothesized to support identifying features of individual entities. In addition, the iAG has been associated with episodic memory (Binder et al., 2009; Maguire, 2012; Svoboda et al., 2006). With respect to semantic category word fluency (regressing out general speech rate), we observed a robust interaction effect

between *semantic category word fluency* and region such that the iAG was much more strongly associated with reduced scores than the aSTS. This suggests that subjects may navigate the task by retrieving animal names based on episodic memories involving animals and/or course thematic relations among entities, without needing to retrieve finer taxonomic features. This would predict that a similar task, for instance requiring subjects to identify all of the features of a particular animal or specific subtypes of an animal, would result in greater association between lower scores and damage to the aSTS.

While we find that different language-related brain regions are associated with different syntactic and semantic deficits, note that we are not claiming that we will find specific brain regions that correspond to some syntactic tasks but not to *any* semantic tasks, or vice versa. Rather, many supposedly "syntactic" or "semantic" tasks likely engage both mechanisms. Thus, we suggest that a key goal for future research in identifying functional dissociations among regions is to more deeply interrogate the possible syntactic and semantic functions elicited by particular experimental tasks.

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Competing Interests

The authors declare no competing interests.

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