

Same words, different structures: An fMRI investigation of argument relations and the angular gyrus



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ABSTRACT

In fMRI, increased activation for combinatorial syntactic and semantic processing is typically observed in a set of left hemisphere brain areas: the angular gyrus (AG), the anterior temporal lobe (ATL), the posterior superior temporal sulcus (pSTS), and the inferior frontal gyrus (IFG). Recent work has suggested that semantic combination is supported by the ATL and the AG, with a division of labor in which AG is involved in event concepts and ATL is involved in encoding conceptual features of entities and/or more general forms of semantic combination. The current fMRI study was designed to refine hypotheses about the angular gyrus processes in question. In particular, we ask whether the AG supports the computation of *argument structure* (a linguistic notion that depends on a verb taking other phrases as arguments) or the computation of event concepts more broadly. To distinguish these possibilities we used a novel, lexically-matched contrast: noun phrases (NP) (*the frightened boy*) and verb phrases (VP) (*frightened the boy*), where VPs contained argument structure, denoting an event and assigning a thematic role to its argument, and NPs did not, denoting only a semantically enriched entity. Results showed that while many regions showed increased activity for NPs and VPs relative to unstructured word lists (AG, ATL, pSTS, anterior IFG), replicating evidence of their involvement in combinatorial processing, neither AG or ATL showed differences in activation between the VP and NP conditions. These results suggest that increased AG activity does not reflect the computation of argument structure per se, but are compatible with a view in which the AG represents event information denoted by words such as *frightened* independent of their grammatical context. By contrast, pSTS and posterior IFG did show increased activation for the VPs relative to NPs. We suggest that these effects may reflect differences in syntactic processing and working memory engaged by different structural relations.

1. Introduction

Accurately computing the relations between verbs and their arguments, often referred to as 'argument structure', is a fundamental component of language comprehension. For example, in the sentence "the fleet destroyed the planet", the meaning of the sentence centers around the verb, a predicate which denotes a destroying event. Knowledge of the properties of that verb and the grammar of English allows a listener to determine that the two arguments, 'the fleet' and 'the planet', name things in different relations to the event: the fleet carrying out the destroying, and the planet being destroyed. These verb-argument relations are critical for listeners to be able to draw appropriate inferences about the speaker's intended message.¹

Are verb-argument relations different in kind from other linguistic

relations, such as the modification relation between an adjective and a noun in a phrase like 'the exotic planet'? While both argument structure and modification relations contribute to the meaning of a sentence, many linguistic theories have suggested that they rely on distinct mechanisms (e.g. [Kratzer and Heim, 1998](#)). Furthermore, there is evidence from cognitive neuroscience that the processing of verb-argument relations may rely on specialized neural machinery. The goal of the present study was to further investigate the possibility of neural specialization for such distinct linguistic mechanisms through a functional magnetic resonance imaging (fMRI) experiment that directly compares the neural response to lexically matched verb phrases ('destroyed the planet'), involving overt verb-argument relations, and noun phrases ('the destroyed planet'), involving modification relations.

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¹ For a clear and exhaustive discussion of argument structure in language, see [Williams \(2015\)](#).

1.1. Argument relations: linguistic and conceptual distinctions

At the outset, it is important to distinguish verb-argument relations (a linguistic notion) from event-participant relations (a conceptual notion). In the absence of overt language, humans can conceptualize events—such as when watching a silent video of a planet being destroyed by a fleet. It similarly seems likely that humans can represent abstract event concepts independent from language; for example, through experience developing an “eating” concept of an event that has two core participants, something that is eating and something being eaten. We will use the term *conceptual arguments* to refer to core participants of an event concept, although we note that in practice it is famously difficult to determine what is the line that divides ‘core’ from ‘non-core’ participants in an event concept, or whether there is such a line at all (e.g., should optional tools like chopsticks be considered ‘core’ participants in the “eating” concept or not?).

Turning to language, it seems that some parts of a sentence are specifically permitted or required by their grammatical context, in other words ‘filling a slot’ in the structure they enter. These we call *argument categories*. A *syntactic argument* fills a syntactic slot in its context, while a *semantic argument* fills a semantic slot. Take ‘destroy the planet’. Here we might say that ‘destroy’ is the kind of verb that can occur in *transitive verb phrases*, with a direct object, and in turn that ‘the planet’ is licensed as a direct object in relation to this fact. This would make ‘the planet’ an argument syntactically. Semantically, we might say that ‘the planet’ names a planet, x , that its grammatical context names the relation of being destroyed, R , and that their combination is interpreted as x satisfying R , $R(x)$. Then ‘the planet’ would be an argument semantically as well.²

Other parts of a sentence seem not to be arguments, and thus to be *adjuncts* instead. By assumption, an adjunct is not permitted or required by specific features of its grammatical context. Instead it is permitted in any phrase of a certain general category, such as the general syntactic category of *verb phrase*, or the general semantic category of *event predicate*. In ‘destroy the planet with a laser,’ for example, we might say that ‘with a laser’ is not an argument but an adjunct. This would be to say, either syntactically or semantically, that it does not fill a slot specifically determined by the category of its immediate context. The transitive verb phrase ‘destroy the planet’ does not specifically permit or require a ‘with’-phrase, nor does it express a relation satisfied by instruments.

How these twin distinctions are encoded differs across grammatical theories. But commonly, information about possible arguments in a verb phrase, or a noun phrase, is encoded in lexical features of the verbs or nouns that head them.³ For example, the verb ‘destroy’ might lexically carry a specific ‘subcategorial’ feature which requires it to combine with a noun phrase, such as ‘the planet’, given only highly general rules of syntactic composition (Chomsky, 1981, 1995; Pollard and Sag, 1994; Bresnan, 2001; Steedman, 2000). And semantically, the verb might express a relation which, given only highly general rules of semantic composition, will entail that its direct object names something that satisfies this relation (Klein and Sag, 1985; Kratzer and Heim, 1998). On this view, VP adjuncts are then parts of the VP that are not licensed or interpreted in relation to specific features of its verb, but instead the structure via rules that will apply to any VP at all. For example, we might say that ‘with a laser’ can combine syntactically with any sort of verb phrase, and always be interpreted by conjunction (‘and

the event was with a laser’).

Independently of argument structure, however, verb phrases also tend to denote different concepts from noun phrases. For example, Gentner and Kurtz (2005) draw a key distinction between entity concepts, which refer to objects and are characterized by their properties, and relational concepts, which refer to relations between things (such as events) and are characterized by their relational structure. Most verb phrases denote events or states, i.e. relational concepts, while most noun phrases denote entity concepts. Therefore, a neuroimaging experiment aiming to isolate the effect of argument structure by comparing verb phrases to noun phrases with modifiers likely conflates the effect of argument structure with the conceptual distinction between events and entities. The present experiment was designed to help deconflate these two dimensions, particularly with respect to the brain area that is commonly implicated in verb-argument structure processing: the angular gyrus.

In this manuscript, we will define “relational processing” as a general term encompassing both event/relational concepts and the linguistic argument structure relations between verbs and arguments, given the general ambiguity regarding the function of the angular gyrus with respect to these possible functional roles.

1.2. Relational processing and the angular gyrus

Neuroimaging and neuropsychological research across the last several decades has identified several left hemisphere brain regions that are critical for language, including the anterior temporal lobe (ATL), the posterior superior temporal sulcus (pSTS), the inferior frontal gyrus (IFG), and the angular gyrus (AG). All of these regions have been shown to demonstrate increased activity for sentences vs. unstructured lists (Pallier et al., 2011; Fedorenko et al., 2012; Matchin et al., 2017), making them good candidates for involvement in combinatorial computations. Among these, it is the AG that has most frequently been suggested to specifically support argument structure computations. While there is good evidence that the AG supports relational processing of some kind, the evidence does not clearly discriminate between a role in processing argument structure per se or rather event concepts. In fact, it is possible that the AG supports argument structure processing via a role in relational concepts, which are likely accessed during the processing of argument structure.

Many neuropsychological studies using the voxel-wise lesion-symptom mapping technique (VLSM) have found a general association between damage to AG, or degeneration of AG, with sentence comprehension deficits (Dronkers et al., 2004; Mesulam et al., 2015; Pillay et al., 2017; Magnusdottir et al., 2013; Rogalsky et al., 2018). Three studies in particular suggest a role more specifically in relational processing.

First, Thothathiri et al. (2012) identified the lesion distributions associated with errors in interpreting semantically reversible sentences like *The man was served by the woman*. Reversible sentences require subjects to correctly assign the thematic roles denoted by the verb, as subjects cannot correctly guess the meaning of the sentence based solely on individual arguments and the events that these arguments typically engage in. They found a strong correlation between damage to the left temporoparietal junction (TPJ), including AG, and deficits in correct argument assignment. Second, a VLSM study of picture naming by Schwartz et al. (2011) found that damage to the AG was associated with thematic substitution errors (e.g., substituting *worm* for *apple*) while damage to the ATL was associated with taxonomic substitution errors (e.g., substituting *pear* for *apple*) (Schwartz et al., 2011). Finally, another VLSM study using eye-tracking by Mirman and Graziano (2012) found that patients with damage to posterior temporal-parietal cortex including the AG had reduced and delayed activation to thematic competitor pictures (e.g. looking at a pig when the target is *barn*) compared to both healthy controls and patients with a more anterior lesion distribution.

² Notice that we allow for arguments to be optional. What matters is only that they are permitted or interpreted with respect to specific syntactic or semantic properties of their immediate context.

³ The alternative is to say that the features licensing an argument are encoded in a structure, possibly silent, which combines both with that argument and with the verb or noun. This structure may be either a morpheme or a construction.

Additional evidence regarding a role for AG in relational processing comes from neuroimaging studies. Two fMRI studies that examined processing of different levels of sentence structure (word lists, phrases, and full sentences) found that AG appeared to selectively activate for full sentences, in contrast to ATL which showed a graded pattern in which activity increased steadily with phrase size (Pallier et al., 2011; Matchin et al., 2017). This is consistent with the view that activity in AG is primarily driven by the thematic relations denoted in a sentence while the ATL plays a more general role in semantic relationships that hold in phrases of all sizes. Some neuroimaging studies have found a more specific relation between thematic processing and activation in the AG. For instance, the fMRI study by Boylan et al. (2017) found evidence that both left and right AG showed larger differences from baseline for relational compounds (e.g., *wood stove*, thematic relationship between words) than attributive compounds (e.g. *bullet train*, feature relationship between the words). By contrast, the ATL showed similar activation for the two types of compounds but with a later peak for the thematic type. An fMRI study by Boylan et al. (2015) found similarity in activity patterns in the left AG for two-word phrases sharing the same verb (e.g., *eats meat* & *eats quickly*), but not for phrases sharing the same argument but with a verb vs. a preposition (*eats meat* & *with meat*), suggesting that the relational information specifically denoted by the verb drives activity in AG rather than conceptual features of the noun phrase, which would be the same whether encoded by a verb or by a preposition. Williams et al. (2017), using MEG, compared noun phrases either high or low in relationality (*director's child* vs. *director's chair*), finding that higher relationality activated inferior parietal cortex in the vicinity of the AG. Finally, an fMRI experiment by Kalénine et al. (2009) required participants to make picture-matching judgments about thematic or taxonomic relations; the AG showed increased activity for judgments about thematic relations relative to taxonomic relations.

While the studies reviewed above do not provide direct evidence in favor of a role for argument structure processing in the AG, a number of studies have reported AG effects with more fine-grained manipulations of linguistic structure. Several fMRI studies have found an association between the presence or complexity of a verb's argument structure and activation in the left posterior perisylvian cortex, including AG. Thompson et al. (2007, 2010) and Meltzer-Asscher et al. (2015) conducted single-word lexical decision experiments in fMRI and showed that activity in the AG and neighboring temporal cortex increased with the number of arguments required by a verb: verbs with three arguments (e.g., *put*) activated these regions more than verbs with two arguments (e.g., *chase*), which activated these regions more than verbs with one argument (e.g., *sleep*). Based on this and other imaging and patient work, they propose that inferior frontal regions are involved in selecting the appropriate syntactic frame for a verb, and that posterior regions (including AG and posterior middle temporal gyrus) are involved in integrating lexical material that satisfies the argument structure requirements. A similar experiment by Meltzer-Asscher et al. (2013) found that verbs with alternating transitivity (e.g., *break* can occur with one argument, as in *the statue broke*, or with two arguments, as in *the child broke the statue*) activated left AG more than verbs that solely occur with one argument (e.g., *bark*), further increasing the association of the AG and verbal argument structure processing.

Some of these studies provide evidence regarding syntactic vs. semantic argument structure effects. The generalization from these studies is that there is consistent activation in AG and nearby surrounding tissue for semantic argument structure complexity independent of syntactic realization. For example, Shetreet et al. (2010) in Hebrew tested a number of comparisons using verbs varying in their syntactic argument structure possibilities and realizations, finding consistent activation for argument structure complexity in the close vicinity of AG regardless of overt syntactic structure realization. Meltzer-Asscher (2015) and Maljutina and den Ouden (2017) found activations in or around AG for argument structure complexity, but failed to find

increased activation for verbs that can be realized with either one or two overt arguments (e.g. *he broke the vase* vs. *the vase broke*) compared to verbs that have only one such option. This suggests that effects reported in AG reflect complexity of deeper underlying semantic argument structure that is not modulated by the particular syntactic realization of those arguments. Interestingly, Shetreet et al. (2007) compared Hebrew verbs that had two possible syntactic argument structures to realize the same semantic argument vs. those that had only one possible syntactic option (that is, controlling semantic argument structure and varying syntactic realization). They found increased activity for multiple syntactic options in the pSTS and superior/posterior IFG but not in AG. These results suggest that while both the posterior temporal lobe and AG show argument structure effects (see also Ben-Shachar et al., 2003), syntactic argument structure may be more associated with pSTS and semantic argument structure may be more associated with AG.

These studies suggest that the association between the AG (as well as the pSTS) and relational processing may be driven by specialized linguistic operations for verb-argument structure. However, most of these studies have compared different verbs to each other – therefore these effects may actually be driven by the activation of event or relational concepts. Recent neurophysiological work using single words has tentatively indicated different localization of activity based on the event/entity distinction, even when this cross-cuts the noun/verb distinction (Bedny et al., 2014; Lapinskaya et al., 2016). In fact, Chatterjee and colleagues have suggested that event concepts are supported by brain regions such as the AG that are located nearby regions for visual motion and actions (Kable et al., 2005; Wu et al., 2007). Under such a view, experiments showing effects of argument structure in the AG actually reflect event concepts accessed by verbs. Under this hypothesis, the AG plays multiple roles in different functional networks – it could support both linguistic argument structure processing and more general conceptual-semantic processing via its activation of event/relational concepts that are associated with particular verbs.

A further complication is that the AG may be involved in a more general form of conceptual-semantic processing. For instance, several studies have shown that the AG shows increased activation for isolated real nouns relative to pseudowords (Binder et al., 2003, 2005; Bonner et al., 2013), and increased activation for concrete nouns relative to abstract nouns (Binder et al., 2005). Relatedly, while Pillay et al. (2017) found an association between AG damage and sentence comprehension, they also found an association between AG damage and picture naming; the fact that both effects highlighted AG suggest that this region is involved in a general semantic process underlying both tasks. Given that isolated nouns presumably do not denote events or have argument structure, these results suggest at least some role for non-relational semantics.

Additionally, Price et al., (2015, 2016) used an adjective-noun paradigm to probe AG, where participants needed to judge whether sequences were readily combinable (*plaid jacket*) or not (*moss pony, turnip chapel, fast blueberry*). They found more activity for the *congruous* items in AG, that patients with damage to AG were less accurate in the judgment, and that subjects with “positive” tDCS to AG were faster in their judgments. The direction of the imaging results is slightly surprising given that EEG/MEG studies of semantic incongruity find either increased responses for incongruity (e.g. Kutas and Hillyard, 1980; Molinaro et al., 2012) or little difference between conditions (Lau et al., 2016), but this may be a function of the judgment task, which is rare in the EEG/MEG literature. Price et al. suggested that AG plays a critical role in general semantic combination; this role does not appear to be straightforwardly attributable to relational/event semantics or linguistic argument structure given that their materials were simple two-word modifications without verbs. At least one MEG study of adjective-noun combination also reported increased activity for AG (Bemis and Pyllkänen, 2012), although this finding is inconsistent across similar studies (e.g. Bemis and Pyllkänen, 2011; Westerlund and Pyllkänen,

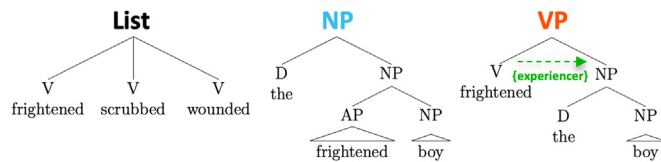


Fig. 1. Example stimuli for each condition, along with an illustration of their corresponding structures. LEFT: the list condition contained unstructured sequences of words derived from the phrases, not involving combinatorial syntax or semantics. MIDDLE: the NP condition, in which the participle adjective (e.g. frightened) adjoins to the noun phrase and modifies its meaning. RIGHT: the VP condition, in which the verb is the head of the phrase with the noun phrase as a syntactically selected complement. The arrow indicates that the verb assigns an experiencer thematic role to the noun phrase as part of the argument structure denoted by the verb.

2014). Similarly, Lewis et al. (2015) reported evidence for processing of both taxonomic and thematic relations in AG, and thus argued that it plays a broader role in semantic combination.

To sum up, while much prior work specifically associates the left AG with processing relational information that has to do with either verb argument structure or conceptual relations between entities and events, other prior work challenges this conclusion by associating this region with more general semantic or conceptual combination. It may be the case that AG plays a role in all of these domains by its connectivity with different functional networks, or it could be the case that there are specialized linguistic processing mechanisms in this region that have not been clearly identified by previous research.

1.3. The present study

The present study was designed to help clarify the extent to which the AG is sensitive to linguistic argument structure. We used a simple paradigm that contrasts the response to lexically-matched verb phrases (VPs) and noun phrases (NPs) in fMRI (see Fig. 1 for examples). We assumed that VPs, such as *frightened the child*, though not a complete sentence, denote events of frightening, e.g. the argument *the child* receives an experiencer thematic role assigned by the verb *frighten*. We compared VPs such as these to NPs formed by taking the verb and switching its order with the determiner. This created phrases such as *the frightened child*, in which the word *frighten* is used as a participle adjective, modifying the noun *child*. Thus, VPs and NPs in this study involved the same root words, denoting similar concepts, but the VPs contain overt argument structure and depict events, while the NPs (without verbs to assign thematic roles) did not. Conversely, NPs involved modification relations while the VPs did not.

According to hypotheses in which AG is involved in processing relational information specific to verbs, increased activity might be predicted in this region for the verb phrase condition over the noun phrase condition, even though the words in each phrase are identical. We included an unstructured word list using the same set of words as in the phrase stimuli as a control to ensure that brain areas showing a difference between VP and NP would also activate for basic combinatorial processing.

Alternative hypotheses about the function of the left AG might predict equivalent activity in the verb phrase and noun phrase conditions. If the AG is involved in processing semantic relations of all kinds, it might respond equivalently to verbal argument structure and adjectival modification. Another possibility is that this region is involved in representing basic lexical semantics for root words that typically refer to events (as opposed to other concepts such as entities). For instance, even though the adjectival form “the frightened child” does not overtly depict an event, the AG may activate because the root word “frighten” typically does refer to an event, or because the meaning of the noun phrase entails an event of frightening.

Finally, we note that while the NP condition does not contain any

overt signal of a predicate-argument relation, some linguistic analyses propose that some or all noun phrases with adjectival participles contain covert (silent) syntactic structure that includes an argument-requiring verbal projection (Bresnan, 1978; Anagnostopoulou, 2003; Bruening, 2014; Embick, 2004; Kratzer, 1994; Meltzer-Asscher, 2010, 2011). For example, participles like “frightened” could have a syntactic structure with the outlines of [X [x FRIGHTEN]], similar to that of a relative clause like “which was frightened”. Under this kind of analysis, the root predicate, “FRIGHTEN”, is sister with a silent noun phrase, here called “x”, that is interpreted as a variable. The combination is then sister to another silent expression, “X”, which induces abstraction over the variable “x”. As a result, and by design, the whole expression has the same extension as “FRIGHTEN” on its own. Both express a predicate that is true of things that were frightened. Therefore, the current study cannot rule out the possibility that if both NP and VP conditions engage the AG, it is because both conditions involve the computation of verbal argument structure, where for the NP conditions this happens as an intermediate step in composing the participle meaning. However, it is important to recognize that even if it were the case that the comprehender infers a complex three-part covert syntactic structure for *frightened* in a nominal context, this does not entail that the comprehender actually chugs sequentially through the composition steps associated with each branch of the structure. In the current case, that would mean something like first saturating the predicate “frighten” with a variable, resulting in the meaning “it was frightened”, and then undoing this saturation via predicate abstraction, to yield a predicate that once again has the same extension as “frighten” to be composed with the noun. While this is a logically possible parsing algorithm, to us it seems much more likely that the parser would simply assign *frightened* the complex description [X [x FRIGHTEN]] in a single step, if this is indeed the correct syntactic analysis of adjectival participles.

The minimal VPs and NPs we constructed for this experiment were specifically designed to test whether the AG processes verb argument structure. However, our materials also contain a fundamental syntactic distinction: a head-complement configuration for VPs, and an adjunction configuration for NPs. This structural distinction might induce increased syntactic processing for either NPs or VPs. Adjunction structures are commonly thought to involve an additional syntactic projection, predicting increased syntactic processing for NPs, while head-complement configurations have been argued to require more syntactic labeling than adjunction structures (Hornstein, 2009), predicting increased syntactic processing for VPs. Additionally, our VP condition involves an open argument slot for the subject position (e.g., *frightened the boy* involves a verb selecting for a subject without that subject being present). This might induce additional processing difficulties for maintaining a phrase with an open slot, compared to the NP conditions which do not have such an open slot.

As our goal was to test functional hypotheses about brain regions previously associated with sentence comprehension, we used a sentence processing localizer to select five regions of interest (ROIs), testing whether any of these regions showed differences among our conditions: the angular gyrus (AG), the posterior superior temporal sulcus (pSTS), the anterior temporal lobe (ATL), the inferior frontal gyrus, pars opercularis (IFGoper), and a more anterior/ventral portion of the inferior frontal gyrus (IFGant). This allows us to examine AG specifically and compare its response profile to other brain regions that have been previously implicated in combinatorial linguistic processing.

2. Materials and methods

2.1. Subjects

20 right-handed, native speakers of English (12 female, mean age = 22, range 18–27) were recruited for this study and were paid \$25 an hour for their participation. One additional subject was excluded from analyses for falling asleep early in the scanning session. Consent was

acquired from each subject before the study began, and all procedures were approved by the Institutional Review Board of the University of Maryland.

2.2. Stimuli

The main experiment had three conditions: noun phrases (NP), verb phrases (VP), and unstructured word lists (LIST) (Fig. 1). A single stimulus in each condition consisted of a sequence of three words. In the NP condition, the sequence consisted of a determiner followed by a participle adjective followed by a noun (e.g., *the frightened child; a scrubbed countertop; our wounded officer*). In the VP condition, the sequence consisted of a verb followed by a determiner followed by a noun (e.g., *frightened the child; scrubbed a countertop; wounded our officer*). In the LIST condition, the sequence consisted of three determiners, three verbs, or three nouns (e.g., *frightened scrubbed wounded; a the our; child countertop officer*). The same set of words was used to generate stimuli for all conditions, with three different experimental lists such that there was no repetition of items for each subject; items were counterbalanced across subjects. The three-word sequences in the VP and NP conditions were identical except for order and an occasional change from “an” to “a” and vice versa as necessary.

To generate these phrases, we first created a large set of three-word sequences that were rated for naturalness by the authors, and we selected only those stimuli that were rated as consistently natural by all the authors to be experimental items for the main experiment. We ensured that both the NP and VP version of each stimulus was natural and coherent. We selected 270 word sequences and then selected 90 for which we created probe stimuli that were used for the subjects’ task, detailed below. These probe stimuli were rated and selected using the same criteria as the main items.

Most studies of structured linguistic materials have used rapid event-related designs, which are most efficient for estimating the hemodynamic response associated with each condition. However, rapid event-related designs have the consequence that the order of conditions is random, so that subjects typically do not know the condition of each trial as it begins. We wanted to ensure that subjects were confident about the identity of each condition as they were processing the probes (e.g., that they would not try to impose structure accidentally on the LIST condition). We therefore used a block design, consisting of six three-word stimuli in a row from the same condition, with a label indicating whether the upcoming block was comprised of NP or VP trials (“PHRASE”) or list trials (“LIST”). We used the set of words from each VP/NP block to create the corresponding LIST block. LIST sequences were created by grouping together the determiners, nouns, and verbs across the VP/NP blocks into their own three-word sequences. This procedure counterbalanced the lexical material used in each block across the conditions while removing linguistic structure from the LIST condition. The order of sequences within each block was randomized for each condition. Stimulus blocks were counterbalanced across conditions; the same set of sequences was used in the corresponding block across the NP, VP, and LIST conditions.

2.3. Task and procedure

The subjects’ task was to make a semantic synonymy/similarity judgment to probes that were presented twice per block, one probe after the first three sequences and one probe after the last three sequences. The probe was a modified version of one of the preceding sequences; one word in the probe was replaced with a different word, the other two words being identical. The replaced word was always either the noun or the verb. The word was replaced with one that was either semantically similar (roughly synonymous) or dissimilar to it. E.g. “the tired man” -> “the exhausted man” (similar) or -> “the frightened man” (dissimilar). The subjects were instructed to press a button to indicate whether the probe, evaluated as an entire phrase, was semantically

similar to one of the preceding items or not. The sequence that was probed was randomly selected, with a roughly equal mix of first, second, and third sequences being probed. Similar and dissimilar probes occurred with equal frequency. The probes for the LIST items were somewhat different from the NP and VP items; for these items we developed probes using the same procedure, but since the LIST sequences were unstructured, the semantic judgment was restricted to the replaced word. E.g. “fans treaty bystander” -> “fans agreement bystander” (similar) or “defendant corpse phone” -> “defendant equipment phone” (dissimilar). This led to a substantial increase in difficulty performing the task, which we address in the discussion. Subjects made their responses using two button boxes, one in each hand; mapping of similar/dissimilar to hand was counterbalanced across subjects.

We explained to subjects the nature of the stimuli and task and trained them on a practice run before they entered the scanner. This practice run was identical to the experiment runs except for being outside the scanner with materials not used in the main experiment, and it was the same for every subject. It consisted of three six-sequence blocks of each condition in random order. Following this practice session, subjects were placed in the scanner. Before beginning the main experiment, they were given one block of each condition from this practice session to re-familiarize them with the task.

The main experiment consisted of 15 blocks from each condition, divided into 5 experimental runs of 3 blocks from each condition. In addition, there were 3 blocks of blank screen (rest) presented in every experimental run to estimate baseline activation; every run ended on a rest block in order to allow the hemodynamic response to return to baseline. We gave subjects a short break in-between runs. The experiment lasted about 1 h and 15 min.

We presented the experiment visually using the PsychToolBox Matlab package (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). The screen was black and the font was white. Each trial block began with a fixation cross presented for a random jittered duration, either 1.5, 2.5, or 3.5 s (with uniform frequency among jitter durations) (1350–3350 ms on, 150 ms blank), and then a label that said either “PHRASE” (VP and NP conditions) or “LIST” (LIST condition) which appeared on the screen for 2 s (1850 ms on, 150 ms blank). We presented these cues so that subjects would be prepared for that condition and adapt their expectations appropriately. The condition cue was followed by 1 s of fixation (850 ms on, 150 ms blank), and then the first sequence of the block started. All words were presented with rapid serial visual presentation, with each item appearing for 600 ms (450 ms on, 150 ms blank). After each sequence was fixation for 1.5 s (1350 ms on, 150 ms blank). After three sequences and fixation periods, the probe in green font appeared on the screen for 2.85 s (2700 ms on, 150 ms blank), followed by the fixation (1.5 s) preceding the next three-word sequence. We instructed the subjects to make their response to the probe at any point before the fixation cross reappeared. Each block lasted a total of 29.5 s, not counting the variable (jittered) fixation that preceded the onset of each block. The REST periods consisted of an initial non-jittered fixation of 1.5 s (1350 ms on, 150 ms blank), the label for 2 s (1850 s on, 150 ms off), a blank screen for 13 s, followed by a numerical countdown from 5 to 1, 5 s total in duration (850 ms on, 150 ms blank per number), that allowed subjects to get ready for the next block. The rest block lasted a total of 20 s, not including the 1.5 s initial fixation. A schematic of the experimental design is presented in Fig. 2.

2.4. Sentence processing localizer

Before the main experiment we presented subjects with a short sentence processing localizer run in order to derive independent ROIs for analysis of the main experiment. This run consisted of sentences taken from Rogalsky and Hickok (2008) as well as unstructured word lists that were created by randomizing the order of words in each sentence. Sentences and lists were presented in random order but with a label to indicate whether the upcoming stimulus was a sentence or list.

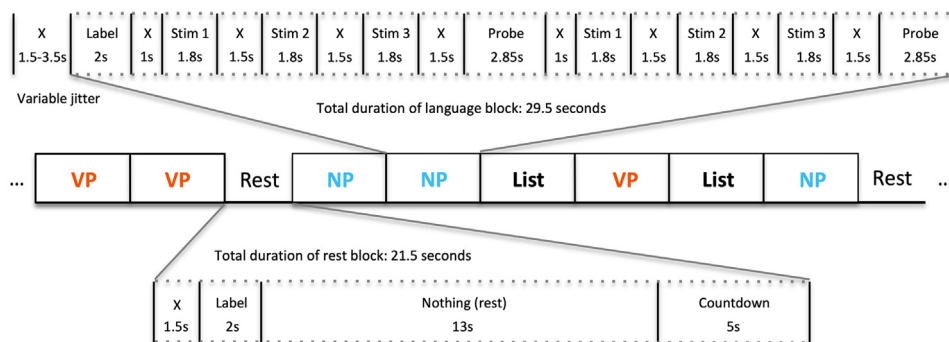


Fig. 2. Schematic of stimulus presentation. MIDDLE: illustration of the sequence of blocks within a run. TOP: timing of stimuli within a given block. BOTTOM: timing of stimuli for the rest blocks.

For sentence trials, the subjects' task was to detect an occasional sentence that was semantically anomalous (we removed these trials from our analysis). These responses were cued with a prompt, "MAKE SENSE?". For the word list condition, the subjects' task was to determine whether a probe word was present in the word list or not. Subjects made their responses using two button boxes, one in each hand; one for "yes" and one for "no", for both the sentence and word lists tasks. I.e., if subjects responded "yes" if the sentence made sense with their right hand, they responded "yes" if the probe word was present in the preceding stimulus also with their right hand. Mapping of yes/no to hand was counterbalanced across subjects.

We started with a set of 40 sentences, and scrambled the order of words to create the list conditions. We then created two stimulus lists that included word lists that did not overlap with sentences, and counterbalanced across subjects. We presented stimuli using rapid serial visual presentation. The condition label appeared on the screen for 1.3 s (1050 ms on, 250 ms blank), then each word was presented for 600 ms (450 ms on, 150 ms blank), followed by fixation for 900 ms (750 ms on, 150 ms blank). The probe was presented on the screen in green font for 1700 ms (1550 ms on, 150 ms blank). We instructed subjects to make their responses while the probe was still on the screen. Following each trial was a random fixation for a minimum duration of 900 ms, variable from 0.9 s to 15 s, optimized to estimate the hemodynamic response using FreeSurfer's OPTSEQ program (<https://surfer.nmr.mgh.harvard.edu/optseq/>). The localizer run lasted about 10 min.

2.5. fMRI data collection and analysis

MR images were obtained in a Siemens TRIO 3T scanner (Siemens Medical Systems) using a 32-channel head coil. We first collected a high-resolution T1-weighted anatomical image in the axial plane (voxel dimension: 0.45 mm × 0.45 mm × 0.9 mm). We then collected a total of 1203 T2*-weighted EPI volumes over 6 runs (1 localizer run of 298 volumes, 5 experimental runs of 181 volumes apiece). Each volume contained 36 oblique slices oriented approximately 20° clockwise relative to the AC-PC axis (TR = 2 s, TE = 25 ms, flip angle = 90°, in-plane resolution = 3 mm × 3 mm, slice thickness = 3 mm with 0.3 mm gap). The first four volumes of each run were collected before stimulus presentation and discarded to control for T1 saturation effects. Slice-timing correction, motion correction, and spatial smoothing were performed using AFNI software (Cox, 1996; <http://afni.nimh.nih.gov/afni>). Motion correction was achieved by using a 6-parameter rigid-body transformation, with each functional volume in each run first aligned to a single volume in that run. Functional volumes were aligned to the anatomical image, and subsequently aligned to Talairach space (Talairach and Tournoux, 1988). Functional images were resampled to 3 mm isotropic voxels, and spatially smoothed using a Gaussian kernel of 6 mm FWHM.

First-level analyses were performed on each individual's data using

AFNI's 3dDeconvolve function. The regression analysis was performed to find parameter estimates that best explained variability in the data. Each predictor variable representing the timecourse of stimulus presentation was entered into a convolution analysis using a canonical hemodynamic response function (AFNI's BLOCK parameter). For the localizer experiment, we modeled the three conditions (list, good sentence, anomalous sentence). For the main experiment, we included a regressor for each condition (VP, NP, and LIST), modeling the duration of the three consecutive phrases within each half of the block separately. We added one regressor for the condition labels that preceded each language block including the preceding and following fixation cross. We added another regressor for the condition labels that preceded the rest block, including the preceding fixation period. We also modeled the 5 s countdown period at the end of the rest block, and modeled the two task portions of each language block, including the following fixation cross for the first task portion. The six motion parameters were included as regressors of no interest.

To perform the group-level analysis, we first identified ROIs from the sentence processing localizer task. We entered the parameter estimates for the sentence and list conditions for each subject into AFNI's 3dANOVA2 function and identified ROIs using the following contrasts: sentences > rest, and sentences > word lists. We used a voxel-wise threshold of $p < 0.005$ (one-tailed) and a small volume correction of 20 voxels in order to identify significant clusters. This threshold resulted in a corresponding False Discovery Rate q value < 0.05 for both of these comparisons, indicating that these results passed a correction for multiple comparisons. We used the same voxel-wise threshold to ensure that the clusters were of approximately the same size for both contrasts. We then selected the following left hemisphere clusters from the whole brain analysis as ROIs from the sentence > list contrast: anterior temporal lobe (ATL), inferior angular gyrus (AG), and inferior frontal gyrus (IFG anterior), straddling the *pars triangularis* and *pars orbitalis*. From the sentence > rest contrast, we selected the pSTS cluster and the portion of the IFG cluster that centered on the *pars opercularis* (IFG opercularis), manually removing voxels lying outside the *pars opercularis*. We then averaged the estimated percent signal change values for each condition of the main experiment (LIST, VP, NP) for each subject within each ROI using AFNI's 3dmaskave, and then ran pairwise comparisons among all the conditions.

To ensure that our ROI analyses were not missing significant effects in the main experiment, we also performed whole brain analyses by entering the parameter estimates for all conditions and subjects into AFNI's 3dANOVA2 function. We performed the contrasts of VP > LIST, NP > LIST, VP > NP, and NP > VP, using two statistical thresholds. First, we performed a standard cluster-size correction for multiple comparisons. We used a voxel-wise threshold of $p < 0.005$ (two-tailed). To obtain a cluster-size threshold, we estimated the smoothness (spatial autocorrelation function) in each subject's data. We used AFNI's 3dFWHMx function and the -acf option to analyze the residual error

terms from each subject’s first-level analyses, averaged the estimated parameters, and entered them into AFNI’s 3dClustSim function to obtain a cluster size correction of 52 voxels. Second, we performed a liberal voxel-wise threshold of $p < 0.01$ (two-tailed) and a cluster size correction of 20 voxels. We used this liberal and uncorrected threshold in order to ensure that no effects that might compromise our ROI analyses or strict whole-brain analyses were left hidden, and as information for future researchers who might seek to perform a similar experimental manipulation. For clarity of presentation, we mapped the whole-brain reduced threshold activation maps to the cortical surface using SUMA (Saad and Reynolds, 2012).

3. Results

3.1. Behavioral performance

For all behavioral analyses, we performed all three planned pairwise comparisons among conditions using two-tailed t -tests and a Bonferroni correction for multiple comparisons (adjusted alpha of $p < 0.0167$). Subjects’ accuracy on the behavioral task is shown in Fig. 2, left. Subjects performed significantly better on the NP condition relative to the List condition: $t(19) = 5.529$, $p < 0.001$ (two-tailed), significantly better on the VP condition relative to the List condition: $t(19) = 4.704$, $p < 0.001$ (two-tailed), with no significant difference between the NP and VP conditions: $t(19) = 1.064$, $p = 0.301$ (two-tailed). These results indicate that the List condition was substantially harder than the two phrase conditions. This effect is likely in large part due to the more extreme working memory burden in the List condition. Overall, these results indicate that subjects were attentive to the task, given the fact that performance on both the NP and VP conditions was higher than a d' of 1.5 (by convention, a d' of 1 is considered good performance), and the List condition was close to 1. The corresponding group average percent correct values for each condition are the following. VP: 77.75%, NP: 75.7%, List: 63.95%.

Response times are shown in Fig. 3, right. Subjects performed significantly faster on the NP condition relative to the List condition: $t(19) = 6.145$, $p < 0.001$ (two-tailed), and significantly faster on the NP condition relative to the VP condition: $t(19) = 2.984$, $p = 0.008$ (two-tailed). The VP condition trended towards being faster relative to the List condition, but this effect did not survive multiple comparisons correction: $t(19) = 2.392$, $p = 0.027$ (two-tailed).

3.2. fMRI: Sentence processing localizer

Table 1 and Fig. 4 report the significant clusters from the localizer analysis. The contrast of sentences vs. rest in the localizer revealed effects in bilateral occipito-temporal cortex, the left pSTS, and a large cluster in the left precentral gyrus and inferior frontal gyrus, with some additional small clusters in the right hemisphere frontal and parietal lobes. The contrast of sentences vs lists revealed significant clusters in

Table 1

Coordinates of significant clusters from the sentence processing localizer analyses. Individual voxel threshold $p < 0.005$ (one-tailed), cluster size threshold of 20 voxels. All voxels passed an FDR correction threshold for multiple comparisons of $q < 0.05$. All coordinates are center of mass (unless noted as local peaks) reported in Talairach space (Talairach and Tournoux, 1988). IFG = inferior frontal gyrus, pSTS = posterior superior temporal sulcus, aSTS = anterior superior temporal sulcus.

Region	Hemisphere	x	y	z	Cluster size (voxels)
<i>Sentence > Rest</i>					
Inferior frontal gyrus/ precentral gyrus	Left	-45	7	33	670
IFG (pars opercularis/ triangularis) peak	Left	-44	13	26	
IFG (pars triangularis/ orbitalis) peak	Left	-50	32	4	
Precentral gyrus peak	Left	-49	-8	50	
Occipito-temporal cortex	Left	-32	-72	-9	653
Inferior occipital gyrus peak	Left	-26	-85	-5	
Fusiform gyrus peak	Left	-39	-46	-13	
Occipito-temporal cortex	Right	31	-77	-8	515
Inferior occipital gyrus peak	Right	25	-86	-4	
Fusiform gyrus peak	Right	41	-60	-10	
Fusiform gyrus peak	Right	36	-40	-15	
Inferior frontal gyrus/ precentral gyrus	Right	42	6	28	110
pSTS	Left	-53	-39	5	71
Medial frontal gyrus	Left	-5	0	57	71
aSTS	Left	-54	-4	-5	33
Inferior parietal	Right	28	-58	35	31
Precentral gyrus	Right	54	-6	44	25
<i>Sentences > Lists</i>					
Superior medial gyrus	Left/right	-4	40	47	399
IFG orbitalis (extending into temporal pole)	Left	-43	25	-7	170
Pars orbitalis peak	Left	-34	26	-13	
Angular gyrus	Left	-46	-66	25	127
aSTS	Left	-54	-4	-9	120
aSTS	Right	49	11	-15	83
Ventromedial prefrontal cortex	Left/Right	1	45	-8	76
IFG (pars orbitalis)	Right	42	28	-7	60
Parahippocampal gyrus	Left	-27	-32	-11	50
Precuneus	Left	-6	-52	21	45
Amygdala	Right	25	-4	-6	20

the left ATL, right ATL, left AG, left IFG (pars orbitalis/triangularis), as well as several medial areas, including the anterior cingulate, ventromedial prefrontal cortex, left precuneus, left amygdala, and left parahippocampal gyrus. Fig. 4 indicates using white circles the significant left hemisphere clusters that were selected for analysis of our main experimental conditions, NP, VP, and List (i.e., the ROIs). From the sentence > list contrast we selected anterior temporal lobe (ATL), inferior angular gyrus (AG), and inferior frontal gyrus (IFG anterior) (straddling the *pars triangularis* and the *pars orbitalis*). From the sentence > rest contrast we selected the pSTS and the IFG (*pars opercularis*).

3.3. fMRI: main experiment

3.3.1. ROI analyses

Table 2 and Fig. 5 provide details of the results of our statistical analyses within the five selected ROIs for the main experiment. In all ROIs except for the IFG *pars opercularis*, we identified significant or near significant effects of the structured conditions (NP and VP) relative to unstructured lists (the VP > List contrast in the AG and the NP > list contrast in the pSTS were not significant). VPs showed significantly increased activity relative to NPs within the pSTS and IFG (*opercularis*),

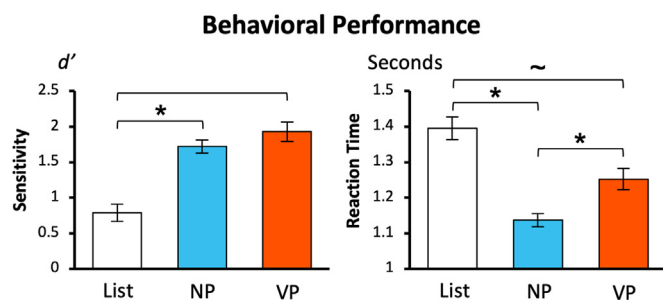


Fig. 3. Behavioral performance during the fMRI experiment. Error bars reflect one standard error of the mean with subject effects removed (Cousineau, 2005). LEFT: sensitivity. RIGHT: reaction time. See text for details of statistical analysis. * = significant effect, ~ = trend towards significance.

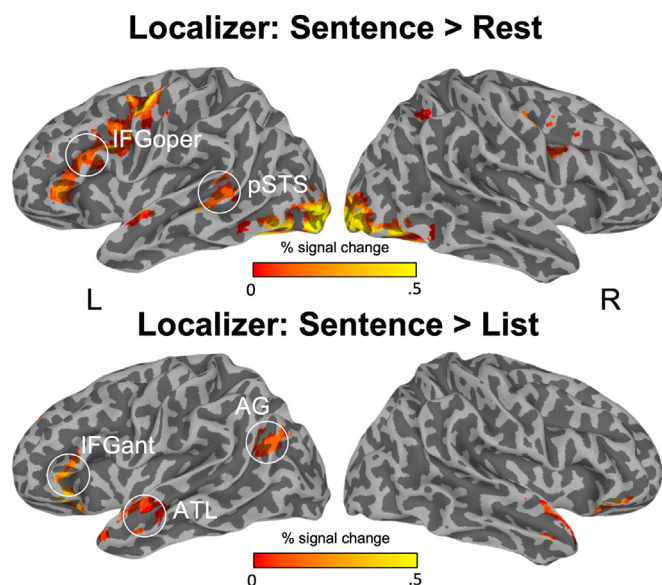


Fig. 4. Whole-brain activation maps for the localizer experiment. TOP: sentence > rest. BOTTOM: sentence > list. Clusters selected to serve as ROIs for the main experiment are shown surrounded by a white circle with their corresponding anatomical labels. Activations are displayed on an inflated template brain in Talairach space (Talairach and Tournoux, 1988). IFGoper = inferior frontal gyrus, *pars opercularis*, pSTS = posterior superior temporal sulcus, IFGant = inferior frontal gyrus, anterior portion, ATL = anterior temporal lobe, AG = angular gyrus.

Table 2

Statistical results of the ROI analyses. * indicates a significant effect when corrected for multiple comparisons, ~ indicates a trend towards significance. All comparisons were two-tailed. Significance is corrected for multiple comparisons with a family-wise alpha threshold of $p < 0.05$ (each region is defined as a separate family), using a Bonferroni correction with an individual p threshold of $p < 0.0167$. IFG = inferior frontal gyrus, pSTS = posterior superior temporal sulcus, ATL = anterior temporal lobe, AG = angular gyrus.

Region	NP vs. List	VP vs. List	VP vs. NP
AG	$t(19) = 3.451$ * $p = 0.003$	$t(19) = 2.279$ ~ $p = 0.034$	$t(19) = -0.326$ $p = 0.748$
pSTS	$t(19) = 1.883$ ~ $p = 0.075$	$t(19) = 4.054$ * $p < 0.001$	$t(19) = 2.790$ * $p = 0.012$
ATL	$t(19) = 3.052$ * $p = 0.007$	$t(19) = 3.277$ * $p = 0.004$	$t(19) = 0.466$ $p = 0.646$
IFG (anterior)	$t(19) = 3.283$ * $p = 0.004$	$t(19) = 4.232$ * $p < 0.001$	$t(19) = 1.817$ ~ $p = 0.085$
IFG (opercularis)	$t(19) = -1.259$ $p = 0.235$	$t(19) = -0.449$ $p = 0.658$	$t(19) = 2.750$ * $p = 0.013$

with a non-significant trend in anterior IFG. By contrast, the AG and ATL regions showed no evidence of any differences in activation between the NP and VP conditions.

3.3.2. Whole-brain analyses

We performed whole brain analyses for the following contrasts: VP > list, NP > list, and VP - NP, using two statistical thresholding procedures: the first with a strict thresholding procedure correcting for multiple comparisons across the whole brain, and the second with an exploratory reduced threshold. We performed this exploratory analysis because we wanted to ensure that any differences we obtained in our ROI analyses were interpretable in light of the whole-brain contrasts. For instance, if the contrast between these conditions resulted in overall greater activity for one condition across many brain areas, the differences between NP and VP we obtained in the pSTS and IFG ROIs would be less meaningful. We have included figures for the reduced threshold

analyses only given the limited number of significant clusters revealed with the strict thresholding procedure. In the tables reporting the size and location of significant clusters, we have indicated the clusters that survived strict thresholding by highlighting those regions in bold and indicating the cluster size in parentheses next to the cluster size identified in the exploratory analyses.

In the exploratory analysis, the NP condition showed increased activity relative to the List condition in bilateral ventromedial prefrontal cortex, left angular gyrus, and less robust activation in bilateral temporal lobe and anterior/inferior IFG, biased to the left hemisphere (Fig. 6; Table 3). Only the ventromedial prefrontal cortex and angular gyrus activity survived the strict thresholding procedure. In the exploratory analysis, the VP condition showed increased activity relative to the List condition in a typical left hemisphere language network: the pSTS, the ATL, and the IFG (pars triangularis/orbitalis) (Fig. 7; Table 3). With the strict thresholding procedure, only the IFG and pSTS clusters were revealed.

In the exploratory analysis of VP vs. NP, VP showed increased activity in pSTS, IFG (pars opercularis/pars triangularis), and dorsal premotor cortex, a similar but not identical pattern to the contrast of VP > List (Fig. 8; Table 4). None of these clusters survived the strict thresholding procedure. NP showed increased activity in a bilateral network that roughly corresponded to the default network: dorsal AG, ventromedial prefrontal cortex, and precuneus, with only the ventromedial prefrontal cortex cluster surviving the strict thresholding procedure.

4. Discussion

The current fMRI study was designed to investigate the extent to which left hemisphere brain regions that show increased activity for structured language input (pSTS, ATL, AG and IFG) are involved in computing overt verb argument structure vs. modification relations. Replicating prior work (Pallier et al., 2011; Fedorenko et al., 2012; Matchin et al., 2017), we found that all of the left hemisphere language-related regions we tested except for the pars opercularis showed a basic structural effect: significantly increased activity for lexically-matched verb phrases (VPs) and noun phrases (NPs) relative to lists, or a trend towards this effect. However, only pSTS and posterior IFG showed increased activity for VPs relative to NPs; there was also a non-significant but suggestive trend for this effect in anterior IFG. Notably, although AG has often been associated with relational processing (argument structure and/or event concepts) in the literature, we did not observe any differences in the response to VPs and NPs in this region. We discuss our results by region, focusing first on the AG.

4.1. The role of the AG in processing argument structure and event semantics

Previous work has demonstrated that AG and surrounding temporal cortex is sensitive to verbal argument structure, showing increased activity in response to verbs that require more arguments (Thompson et al., 2007, 2010; Meltzer-Asscher et al., 2012, 2015; Malyutina and den Ouden, 2017). The current results suggest that these effects do not directly reflect overt argument structure, as we observed no difference in the AG response between the VP and NP conditions. However, the fact that both types of phrases elicited a larger AG response than unstructured word lists is consistent with previous work implicating the AG in combinatorial and/or conceptual-semantic processing (Price et al., 2016; Boylan et al., 2015; Binder et al., 2009; Pallier et al., 2011; Williams et al., 2017).

In the introduction (Section 1.3), we noted that one possible explanation of these results is that the adjectival participles in the NP condition contain *covert* syntactic and semantic structure which triggers equivalent predicate-argument processing operations to those that occur in overt verb phrases. A number of linguistic analyses have

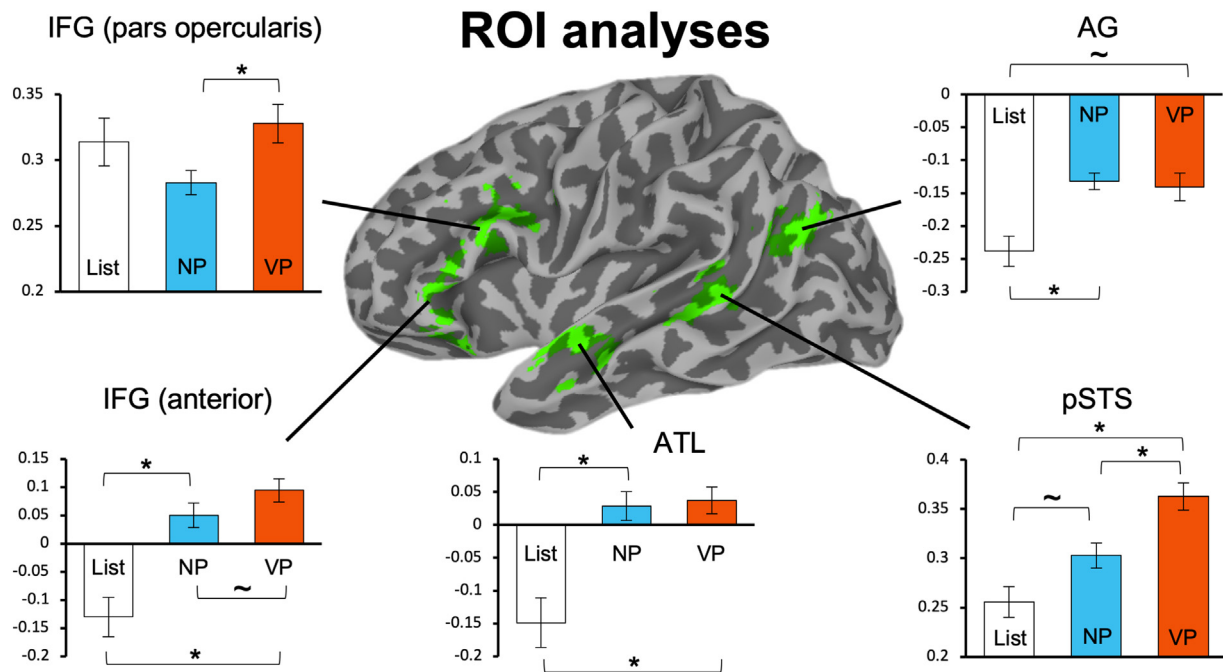


Fig. 5. ROI analyses. ROIs are displayed on an inflated template brain in Talairach space (Talairach and Tournoux, 1988). Error bars reflect one standard error of the mean with subject effects removed (Cousineau, 2005). Details of test statistics are reported in Table 2. * = significant effect. ~ = trend towards significance. IFG = inferior frontal gyrus, pSTS = posterior superior temporal sulcus, ATL = anterior temporal lobe, AG = angular gyrus.

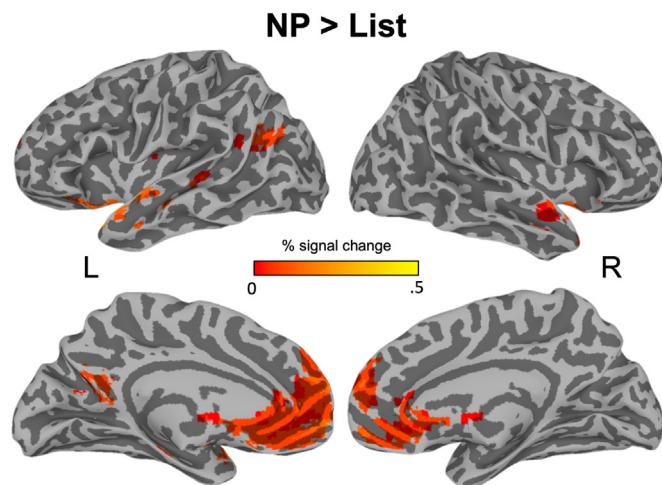


Fig. 6. Whole brain exploratory analyses for the contrast of NP > list. Activations are displayed on an inflated template brain in Talairach space (Talairach and Tournoux, 1988).

posited such covert structure in the representation of the participle (Bresnan, 1978; Kratzer, 1994; Anagnostopoulou, 2003; Embick, 2004; Meltzer-Asscher, 2010; Bruening, 2014). If these analyses are correct, it is possible that the online processing algorithm computes this complex structure step-by-step, such that the saturation of the predicate by a covert variable is computed in the same way as in the VP case, prior to a subsequent step of predicate abstraction. We cannot rule out this possibility and believe it is an interesting question to pursue in future work. However, our own sense is that even if this is the correct analysis of participles, a more plausible online parsing algorithm would be one in which that complex syntactic and semantic structure is assigned in a single step.

Alternatively, the lack of a difference in activation between NPs and VPs in the AG could reflect conceptual processing that is equivalent between the two conditions. As discussed above, one branch of prior

Table 3

Coordinates of significant clusters from the whole-brain analyses of the main experiment for VP > List and NP > List. All regions survived the exploratory individual voxel threshold $p < 0.01$ (two-tailed), with cluster size threshold of 20 voxels (uncorrected for multiple comparisons). Clusters surviving the strict procedure, voxel-wise threshold $p < 0.005$ with cluster size threshold of 52 voxels, are highlighted in bold with corresponding cluster size in parentheses. All coordinates are center of mass reported in Talairach space (Talairach and Tournoux, 1988), unless noted as local peaks.

Region	Hemisphere	x	y	z	Cluster size (voxels)
<i>VP > List</i>					
IFG/aSTS/Anterior cingulate	Left	-35	15	-6	709 (232)
IFG (pars orbitalis) peak	Left	-37	25	-9	
Hippocampus peak	Left	-22	-16	-8	
aSTS peak	Left	-53	-4	-6	
Anterior cingulate peak	Left	-1	38	-6	
pSTS	Left	-48	-39	7	209 (150)
Insula/Inferior parietal	Left	-32	-19	22	85
Superior medial gyrus	Left	-9	52	25	71
Angular gyrus	Left	-42	-61	21	54
Parahippocampal gyrus	Left	-31	-32	-13	37
Temporal pole	Right	48	21	-20	26
Cerebellum	Right	21	-75	-31	25
Heschl's gyrus	Right	41	-17	4	23
Caudate	Left	-13	9	25	23
<i>NP > List</i>					
Ventromedial prefrontal cortex	Left/Right	-2	42	10	995 (741)
IFG (pars orbitalis)	Left	-35	22	-12	189 (114)
Angular gyrus	Left	-43	-58	21	112 (67)
aSTS	Left	-54	-2	-8	94
Precuneus	Left	-7	-56	21	84
Hippocampus	Left	-22	-13	-9	50
Temporal pole	Right	46	19	-17	45
Insula	Left	-31	-17	18	44
pSTS	Left	-46	-33	1	33
aSTS	Right	53	1	-10	30
IFG (pars orbitalis)	Right	29	12	-13	20

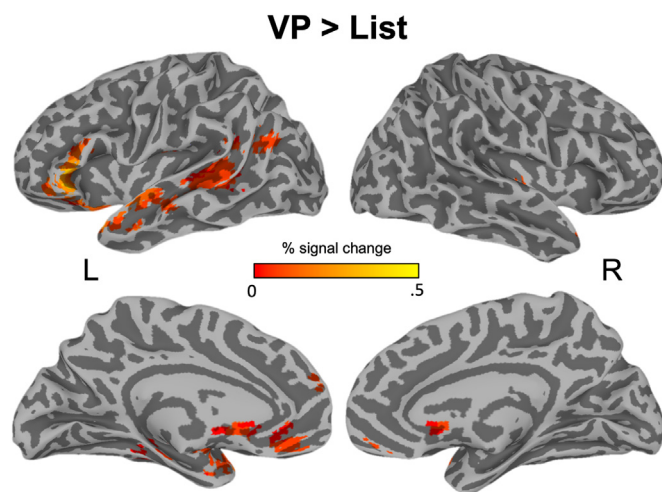


Fig. 7. Whole brain exploratory analyses for the contrasts of VP > list. Activations are displayed on an inflated template brain in Talairach space (Talairach and Tournoux, 1988).

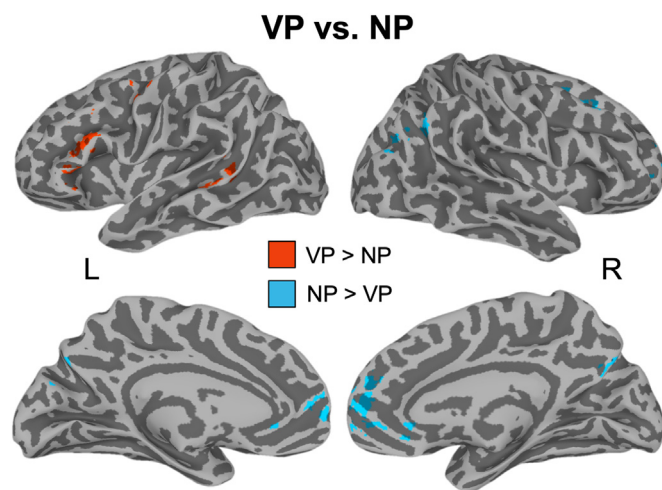


Fig. 8. Whole brain exploratory analyses for the contrast of VP vs. NP. Activations are displayed on an inflated template brain in Talairach space (Talairach and Tournoux, 1988).

work on the AG has suggested that it is broadly involved in general conceptual processing operations that cuts across different types of relations. This idea is supported by studies that report an association between left AG and general conceptual combination using materials that don't include verb-argument combination (Price et al., 2015, 2016; Bemis and Pylkkänen, 2012; 2013; Williams et al., 2017), and studies that observe similar activity in AG for both taxonomic and thematic relations (Lewis et al., 2015; Sachs et al., 2008). The current findings would naturally follow from this account, as both the NP and VP conditions involved generating and representing conceptual relations.

However, we believe the current results are also consistent with previous proposals associating the AG with more specific kinds of conceptual processing, which were driven by the substantial volume of neuroimaging and lesion data associating the AG with event/relational semantics and verb argument structure. These previous findings can be reconciled with the current ones under an account in which AG plays a role in computing and/or accessing conceptual relations between events and participants—in other words, placing the specificity not in representing linguistic verb/predicate-argument relations, but conceptual event-participant relations. To take our own experiment as an illustration, in the noun phrase “the frightened boy”, the root *frighten* denotes an event, and it is conceivable that the lexical access routine

Table 4

Coordinates of clusters from the exploratory whole-brain analyses of the main experiment for VP > NP and NP > VP. All regions survived the exploratory individual voxel threshold $p < 0.01$ (two-tailed), with cluster size threshold of 20 voxels (uncorrected for multiple comparisons). Clusters surviving the strict procedure, voxel-wise threshold $p < 0.005$ with cluster size threshold of 52 voxels, are highlighted in bold with corresponding cluster size in parentheses. All coordinates are center of mass reported in Talairach space (Talairach and Tournoux, 1988).

Region	Hemisphere	x	y	z	Cluster size (voxels)
VP > NP					
Cerebellum	Right	22	-56	-39	65
IFG (pars triangularis)	Left	-50	21	23	58
Cerebellum	Right	17	-64	-22	41
Precentral gyrus	Left	-45	-2	49	29
pSTS	Left	-52	-43	5	26
IFG (pars orbitalis)	Left	-46	26	5	20
NP > VP					
Ventromedial prefrontal cortex	Left/Right	7	51	11	168 (63)
Superior frontal gyrus	Right	26	19	43	45
Precuneus	Right	3	-71	30	30
Angular gyrus	Right	50	-56	29	29
Angular gyrus	Right	38	-67	24	22

that involves retrieving the morphemes that compose the adjective *frightened* may automatically engender activation of this stored event representation. On this account, the left AG may be involved in processing the event information associated with particular words regardless of whether they are used in a syntactic context whose logical form denotes an event or not. In prior studies finding effects of verb argument structure in AG, subjects would likely have accessed the associated event concepts as well. Verbs with more complex argument structures may induce the construction and/or access in memory of more complex event representations, increasing activation in the AG.

From this perspective, the AG would support a variety of tasks, from general semantic processing to verb argument structure computations, via its role in event/relational concepts and its interaction with different functional networks. For instance, the automatic activation of events canonically associated with particular words (or the implicit computation of such events) could explain increased activity in the AG for real nouns relative to pseudowords in lexical decision tasks (Binder et al., 2003, 2005; Bonner et al., 2013) or for “meaningful” semantic combinations relative to less meaningful ones (Price et al., 2015, 2016). For instance, the fMRI study by Price et al. (2015) found that meaningful combinations like *plaid jacket* activated the left AG more than less meaningful ones such as *moss pony*. Plaid jackets are associated with many event representations, such as a lumberjack cutting down a tree or a cocktail party in the 1960s. By contrast, moss ponies are not associated with any event representations. Subjects may assess “meaningfulness” – a somewhat vague notion – by attempting to imagine events involving the depicted entity. If many events come to mind, this could be high “meaningfulness”. If few (or no) events come to mind, this could be low “meaningfulness”. However, our results alone do not provide evidence in favor of event semantic processing in AG; it is important in this context to replicate and extend previous findings suggesting such a role.

Overall, our results help narrow down the functional contribution of this region, suggesting that it does not simply respond to the presence or absence of overt argument structure denoted by a verb. This leaves open the question: how does the brain process linguistic argument structure? Such a question goes beyond the scope of the present investigation. However, the failure to provide good evidence for a plausible neural correlate of linguistic argument relations highlights the need to develop and test more detailed models of linguistic and semantic processing in the brain to pursue this and other questions

regarding the neurobiology of language.

4.2. ATL vs. AG in conceptual-semantic processing

A variety of studies have found notable dissociations between the ATL and the AG. The present study is not one of them, as we found essentially the same pattern of activation in these two regions: increased activation for phrases relative to unstructured lists (replicating a large body of previous work), with no difference between VPs and NPs. The only distinction between these two regions was that in the ATL, the VP and NP conditions produced slightly increased activation relative to baseline, with the List condition well below baseline, and in AG all conditions were well below baseline.

As reviewed in the introduction (Section 1.2), damage to AG is associated with deficits in relational processing (Thothathiri et al., 2012; Schwartz et al., 2011; Mirman and Graziano, 2012). By contrast, damage or degeneration to ATL is associated with deficits in processing the conceptual features associated with entities (Hodges et al., 1992; Schwartz et al., 2011). This roughly corresponds to the double distinction Mesulam et al. (2015) observed between the association of degeneration of ATL with word comprehension deficits, and the degeneration of AG with sentence comprehension deficits. Additionally, neuroimaging studies have identified distinctions between phrase-level activations in ATL and more categorical responses in AG contingent on full sentences (Pallier et al., 2011; Matchin et al., 2017). In the present study, the failure to identify any functional distinction between these regions is likely attributed to the fact that both conditions contained phrase-level combinations, accounting for roughly equal activation in ATL, as well as event concepts or semantic argument structure, accounting for roughly equal activation in AG.

4.3. pSTS: lexical-syntactic processing

The pSTS and anterior IFG showed increased activity for VPs relative to NPs, and increased activation for phrases relative to lists in the main experiment. In principle, this activation could reflect semantic argument structure. However, the pSTS has been previously shown to activate to structured phrases and sentences even when content words have been replaced with pseudowords, which greatly reduces conceptual content (Pallier et al., 2011; Fedorenko et al., 2012; Matchin et al., 2017). This suggests that effects in the STS are not due to semantic argument structure but rather overt syntactic argument structure. This converges with previous fMRI studies that have identified effects of argument structure in the posterior temporal lobe (Ben-Shachar et al., 2003; Shetreet et al., 2007; Malyutina and den Ouden, 2017).

We suggest that the increased activation for VPs relative to NPs in pSTS in the current study is due to the activation of syntactic subcategorization frames stored in this region. All of our verbs were transitive, requiring a noun phrase complement; such information is presumably accessed in computing the syntactic structure of the VPs in this study. However, the adjectival versions of these words do not require any complements; it may be that when these words are clearly adjectives (in NP context), they do not activate the subcategorization information stored on the corresponding verbs. Previous research has associated the posterior temporal lobe with lexical access (see Lau et al., 2008 and Hickok and Poeppel, 2007 for review), consistent with the idea that lexicalized subcategorization information is stored in the pSTS, exhibiting increased activation for verbs with subcategorization relative to adjectives without such subcategorization.

As noted in the introduction, semantic argument structure and syntactic subcategorization are usually confounded. One prior fMRI study by Shetreet et al. (2007) de-confounded these variables through the property of ambiguity, which has been shown to modulate neural activity in the posterior temporal lobe (Rodd et al., 2005; Snijders et al., 2008). They examined verbs that are ambiguous with respect to the

syntactic frames that they can appear in, such as *discover*, which can take a noun complement (*discovered the treasure*) or a sentence complement (*discovered that the earth is round*). Shetreet et al. argue that while in some cases the syntactic ambiguity is associated with thematic ambiguity (for *discover*, the complement is interpreted as either a theme or a proposition), in other cases both syntactic frames convey the same thematic relations (for example, in Hebrew *taste the soup* vs. *taste from the soup*, the complement is always interpreted as a theme). They observed increased activity in posterior temporal lobe (as well as IFG) for verbs with more than one syntactic frame, but this activity was unaffected by the number of thematic options, suggesting that these activations were due to syntactic subcategorization rather than argument structure. If this hypothesis is correct, the increased activation for VPs relative to NPs in our study might be due to the activation of syntactic subcategorization information stored with a lexical item. However, given that our study was not designed specifically to discriminate among these alternatives, we cannot be confident in this interpretation, and more research is needed to determine whether subcategorization is specifically tied to pSTS activity.

Finally, an additional possibility is that increased activity for VPs in pSTS (and posterior IFG) actually reflects a frequency effect rather than a linguistic one. Although the lexical items were controlled across conditions with respect to the root word and overt morphology, it may be that the frequency of usage with respect to syntactic category was different across the NP (adjective usage) and VP (verb usage) conditions. Previous fMRI research has occasionally observed that some left hemisphere regions shows increased activity for low frequency words relative to high frequency words (Fiebach et al., 2002; Kronbichler et al., 2004; de Zubicaray et al., 2005; Hauk et al., 2008), although the presence of this effect depends on task and syntactic context (Keller et al., 2001; Carreiras et al., 2006). Future research could investigate the effect of such contextual frequency effects on brain activation in language areas.

4.4. Anterior IFG

The anterior IFG (pars orbitalis/triangularis) showed a non-significant trend towards increased activation for VPs relative to NPs, with significant increased activation for both kinds of phrases relative to lists. The increased activation for structured phrases relative to lists is consistent with previous research identifying effects of linguistic structure and semantics (Badre and Wagner, 2007; Binder et al., 2009; Pallier et al., 2011; Goucha et al., 2015; Rogalsky et al., 2015; Matchin et al., 2017). We hesitate to interpret the non-significant trend of increased activation for VPs relative to NPs, given that we did not expect an argument structure effect in this region; more data would be needed to determine if this effect is indeed reliable and informative as to the functional role of the anterior IFG.

4.5. The pars opercularis – verbal working memory

The pars opercularis ROI showed a significant increased response to VPs relative to NPs. Given the strong association of this region with syntactic processing in the literature (Ben-Shachar et al., 2003; Snijders et al., 2008; Goucha and Friederici, 2015; Zaccarella et al., 2017), it is tempting to interpret this result as syntactic structure building. However, a large prior literature has attributed the function of the mid-posterior IFG in sentence processing instead to cognitive control and/or verbal working memory resources (Thompson-Schill et al., 1997; Novick et al., 2005; Rogalsky and Hickok, 2011; Matchin et al., 2017). Consistent with this, unlike the more anterior portion of the IFG and the pSTS, activity in this region was actually numerically higher for the list condition relative to the NP condition, and the list condition was almost numerically equal to the VP condition. Given that the list condition did not involve combinatorial processing, and our blocked design likely prevented subjects from mistakenly building structure in these stimuli,

these effects are hard to attribute to syntactic processing.

On the other hand, the somewhat elevated activation for lists relative to NPs in this region fits with a role for this region in verbal working memory and/or cognitive control. Given that unstructured word lists do not allow for efficient chunking to reduce working memory load, while sentences facilitate working memory through syntactic and semantic chunking, the word lists in our study greatly increased demands on working memory resources and/or executive function resources. This is consistent both with the much lower performance on the word list condition relative to the phrase conditions, as well as the informal reports of our subjects that word recall in the list condition was quite hard. The pars opercularis has been previously implicated in verbal working memory tasks, consistent with this explanation (Hickok et al., 2003; Buchsbaum et al., 2011). It is also relevant to note that the reduced threshold whole brain analysis of VP > NP revealed an effect in the dorsal precentral gyrus, which is also strongly implicated in verbal working memory tasks (Buchsbaum et al., 2011).

Conversely, it is somewhat less clear why verbal working memory or cognitive control demands for VPs would pattern with lists relative to NPs, as both VPs and NPs had syntactic and semantic structure that would seem likely to reduce demands on verbal working memory resources. It is worth noting that reaction times were significantly slower for the VPs compared to the NPs, however. At the same time, accuracy in the VP condition was actually numerically higher than in the NP condition, and our own informal impressions and discussions with subjects suggested that the VP condition felt slightly easier to perform than the NP condition. One factor of note is that our VP condition involved the selection for a subject that was missing, which was not the case in the NP condition. E.g., in *frightened the boy*, the verb *frighten* selects for a subject/agent, the doer of frightening, but this argument was absent in the presented material. It is possible that this could have induced some kind of additional working memory burden for VPs over NPs. One could also speculate that the conceptual differences between entities and events result in differences in the resources required to represent them in working memory.

4.6. Greater activation for NPs relative to VPs in ventromedial prefrontal cortex

All of our hypotheses assumed greater linguistic and/or conceptual complexity in the VP condition relative to the NP condition. However, our whole-brain analyses revealed significantly increased activity for the NP condition relative to the VP condition in the bilateral ventromedial prefrontal cortex (Fig. 8, blue). It is tempting to interpret this as potentially reflecting the processing of covert argument structure in the NP condition, given that a previous magnetoencephalography (MEG) study (Pykkänen and McElree, 2007) found increased activity approximately in this region for covert semantic processing, that is increased activity for sentences like "the author began the book" (in which there is an implied activity of reading) relative to sentences like "the author wrote the book", with no implicit reading. However, we note that an fMRI study with the same paradigm (and more precise spatial localization) identified the effect of covert semantic processing in the IFG and not ventromedial regions, suggesting that the MEG study mislocalized the effect (Husband et al., 2011). Given that ventromedial regions are commonly found to be active in rest periods relative to demanding tasks, the so-called default mode network (Binder et al., 1999; Raichle et al., 2001), we rather suggest that the increased activity for NPs in this region relative to VPs is transparently related to the fact that reaction times (and corresponding task-related activity) were greater in the VP condition.

4.7. Conclusions

Our study introduced a novel, fully lexically-matched paradigm to

test whether activity in the left angular gyrus contributes specifically to the computation of overt syntactic argument structure in linguistic input. The lack of difference we observed in the response to VPs and NPs in this region suggests that it does not. However, this pattern is consistent with a role for this region in the processing of event concepts and/or semantic argument structure associated with a given word. Future research should aim to further discriminate between semantic argument structure, event concepts, and more general semantic processing in this region. In addition, the significant increase in activation we obtained for VPs relative to NPs in the pSTS further supports a role for this region in syntactic processing, generally defined (Pallier et al., 2011; Matchin et al., 2017), which may be related to syntactic selection or subcategorization more specifically.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2019.01.019.

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