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Compositionality and the angular gyrus: A multi-voxel similarity analysis of the semantic composition of nouns and verbs

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ABSTRACT

The cognitive and neural systems that enable conceptual processing must support the ability to combine (and recombine) concepts to form an infinite number of ideas. Two candidate neural systems for conceptual combination—the left anterior temporal lobe (ATL) and the left angular gyrus (AG)—have been characterized as "semantic hubs" due to both functional and anatomical properties; however, these two regions likely support different aspects of composition. Here we consider two hypotheses for the role of AG in conceptual combination, both of which differ from a putative role for the ATL in "feature-based" combinatorics (i.e., meaning derived by combining concepts' features). Firstly, we examine whether AG is more sensitive to function-argument relations of the sort that arise when a predicate is combined with its arguments. Secondly, we examine the non-mutually exclusive possibility that AG represents information carried on a verb in particular, whether this be information about event composition or about thematic relations denoted uniquely by verbs. We identified voxels that respond differentially to two-word versus one-word stimuli, and we measured the similarity of the patterns in these voxels evoked by (1) pairs of two-word phrases that shared a noun that was an argument, thus sharing function-argument composition (e.g. *eats* meat and *with* meat), in comparison with two-word phrases that shared only a noun, not an argument (e.g., *eats meat* and *tasty meat*); and (2) stimulus pairs that shared only an event (operationalized here as sharing a verb; e.g. eats *meat* and eats *quickly*), in comparison to both of the above. We found that activity patterns in left AG tracked information relating to the presence of an event-denoting verb in a pair of two-word phrases. We also found that the neural similarity in AG voxel patterns between two phrases sharing a verb correlated with subjects' ratings of how similar the meanings of those two verb phrases were. These findings indicate that AG represents information specific to verbs, perhaps event structure or thematic relations mediated by verbs, as opposed to argument structure in general.

1. Introduction

Language owes its infinite expressive capacity to our ability to take simple building blocks, such as words or concepts, and combine them into complex representations. In linguistics, such "semantic composition" refers expressly to the combination of words into complex linguistic expressions, the meanings of which are a function of both the constituent building blocks (words) and the "rules" used to combine them (the grammar). Whether, and how, such grammatical operations might be realized in the brain are still highly debated questions, and the emergence of compositional meaning from units such as morphemes, words, or concepts, is largely a mystery. However, understanding the engine of compositionality in the brain is a fundamental desideratum to any cognitive neuroscientific model of semantics.

1.1. Roles of left anterior temporal lobe and left angular gyrus in semantic composition

The psycholinguistically motivated neuroanatomical models of semantic processing that have emerged in the past few years involve several brain areas which roughly cluster into four main regions: left inferior frontal, left anterior temporal, left posterior temporal, and left temporo-parietal (Ben Shalom and Poeppel, 2007; Binder and Desai, 2011; Binder et al., 2009; Lau et al., 2008; Pallier et al., 2011; Patterson et al., 2010). Of these regions, there are two – left anterior temporal lobe (ATL) and left angular gyrus (AG) – that are prime candidates to support composition, because both show greater activation for well-formed sentences than for non-compositional lists of words (Pallier et al., 2011, *inter alia*). In addition, both have been characterized as "semantic hubs", owing

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to functional and anatomical patterns that are consistent with multimodal convergence (Binder and Desai, 2011; Lambon Ralph, 2014; Patterson et al., 2007; Seghier, 2012). While the mechanism by which different modalities converge on a single given conceptual representation is still unclear, it is likely that the mechanism that can encode the binding of modality-specific features into a given concept also accomplishes the binding of words into higher-level linguistic constructs (Westerlund and Pylkkänen, 2014). We begin with a brief review of findings relating to composition involving ATL in order to motivate contrasting ideas we will consider in the current study regarding composition in AG.

The ATL is uniquely situated at the end of a caudal-to-rostral stream of information processing feeding from primary sensory and motor areas and association cortex (Binder et al., 2009; Binder and Desai, 2011; Binney et al., 2012; Felleman and Van Essen, 1991). It is thus located at a prime "convergence zone" for inputs from many different modalities. Moving anteriorly along the temporal lobe, one finds a caudal-to-rostral hierarchy emerge as neuronal responses are more tuned to complex stimuli and more invariant to low-level sensory variation; such a hierarchy has been established along both visual (Felleman and Van Essen, 1991) and auditory (Rauschecker and Scott, 2009) streams. This "graded convergence" may provide a mechanism both for "feature combination" and, in the limit, for maximally invariant amodal, and thus abstract, conceptual representations. The culmination of this graded convergence up the temporal lobe (Rauschecker and Scott, 2009; Stringer and Rolls, 2002) is a basal rostral region of ATL shown to have very limited extra-temporal connectivity and high intra-temporal connectivity (Binney et al., 2012). Such neuroanatomical sequestration is arguably a *sine qua non* for a region able to represent abstract, modality-invariant semantics. Thus, ATL is a prime candidate for semantic composition.

In one of the first studies investigating the neural correlates of minimal two-word composition, Baron and colleagues (Baron et al., 2010) found evidence from fMRI pattern analyses that the left ATL subserved the combination of concepts such that the superimposition of individual patterns of the simplex concepts *young* and *man* (as represented by various face stimuli) reliably predicted the activation pattern for the complex concept *young man*. Consistent with this finding, a magnetoencephalography (MEG) study of visually presented two-word phrases comparing nouns in minimal compositional contexts (*red boat*) with nouns in non-compositional contexts (in which a non-word letter string was concatenated with a real word, e.g. *xkq boat*) found increased composition-related activity in left ATL (Bemis and Pylkkänen, 2011). Thus, there is a growing body of functional and tractographic studies to suggest that the left ATL substrate of composition may be multimodal sensorimotor features, and particularly *visual* features of object-concepts (Coutanche and Thompson-Schill, 2014), corroborating the notion of the left ATL as hub of the so-called ventral "what" pathway.

While the left ATL has recently received much attention as a potential semantic hub, it is not the only region to invite this label. Researchers have also ascribed the role of a semantic hub to the AG, as it lies at the junction between temporal, parietal, and occipital lobes and thus receives a confluence of auditory, somatosensory, spatial, and visual inputs. Left AG has been implicated along with left ATL in conceptual combination studies of the sort described above (Bemis and Pylkkänen, 2012), and several studies demonstrate bilateral AG sensitivity to manipulations whereby well-formed sentences are contrasted with word lists, pseudowords, or scrambled sentences (Bavelier et al., 1997; Bottini et al., 1994; Humphries et al., 2007, 2006). Left AG also shows greater activity for connected discourse vs. unrelated sentences (Fletcher et al., 1995; Homae et al., 2003; Xu, Kemeny et al., 2005). This broad profile of effects has led some to suggest that the AG may play a potentially domain-general role in semantic information integration structured around events (Binder and Desai, 2011; Binder et al., 2009; Lau et al., 2008; but cf. Noonan et al. (2013), and Section 4 for evidence that certain sites within AG are involved in semantic control processes, not representations).

Not all studies investigating conceptual combination find activation in both left ATL and bilateral AG. Upon closer inspection of those stimuli that elicit differential activity in AG but not in left ATL, one finds that the type of composition involved is invariably based on thematic relations rather than feature combination *per se*. For instance, Graves et al. (2010) compared familiar meaningful noun–noun pairs, such as *lake house*, with reversed phrases, such as *house lake*, the meanings of which were not obvious; they found that AG, along with other temporoparietal areas (mostly right-lateralized), showed greater activation for processing the more obviously combinatorial phrases. In characterizing the compositional operation employed in interpreting their particular noun–noun stimuli, the authors noted that most of their noun–noun stimuli were interpreted as denoting thematic relations between head and modifier nouns; that is, most compounds consisted of nouns participating in some spatial relation (as in "*a* house *on a* lake") or event-based relation rather than sharing some common feature (as in, for instance, a nominal compound like *cactus carpet*, which is more likely to be interpreted as "*a* carpet *that is prickly like a* cactus" than as some sort of relational compound, like "*a* carpet *with a* cactus *placed on it*") (Estes, 2003; Wisniewski and Love, 1998). This raises the question as to whether these stimuli were probing combinatorial semantics in general, or semantic thematic relations in particular.

In another group of studies, experimenters looking at 1-, 2-, and 3-argument verbs (that is, intransitive, transitive, and ditransitive verbs, respectively) found that activation in bilateral angular and supramarginal gyrus (BA 39 and 40) correlated parametrically with the number of thematic roles that can attach to a given verb, even when the verb was presented in isolation (Meltzer-Asscher et al., 2013; Thompson et al., 2007; Thompson et al., 2010). Whereas Graves et al. (2010) indicates AG involvement in processing spatial and event-based relations, broadly construed, the work on verb adicity suggests a more selective sensitivity to verbs' thematic relations and/or event complexity carried on the verb. While AG has been found to be sensitive to both linguistic event structure and non-verbal events depicted in scenes and mini-movies (Sitnikova et al., 2008a, 2008b), it could be that the verb is the minimal linguistic expression of fundamental thematic relation-based or event-based concepts that AG subserves. This would predict that verb semantics would be particularly privileged in AG semantic space.

1.2. A feature vs. function dichotomy?

Given that both ATL and AG are implicated in semantic composition, we might start with the hypothesis that *any* kind of semantic similarity between two concepts might influence the similarity of neural (in our case, voxel) patterns evoked by the concepts in these two regions. For instance, regions that encode the meaning of a two-word phrase (such as "eats meat") ought to elicit a similar neural response to other two-word phrases that share either of these two words as compared to a phrase that shares none of the words. In this study, we go one step further and explore possible restrictions on this prediction. We suggest that whereas the left ATL may be involved in structuring semantic knowledge around commensurate features of (object-) concepts, the AG builds semantic knowledge based on functional/thematic relations between concepts. Of course, this distinction could be operationalized in a number of different ways. In this study, we test two possible dimensions along which the left ATL and AG