

Remaining Puzzles about Morpheme Production in the Posterior Temporal Lobe

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Abstract—Using data from time-resolved cortical stimulation, intracranial neural recordings, and focal surgical resections, Lee et al. (2018) demonstrate that a small area within left posterior superior temporal gyrus (pSTG) supports the ability to produce functional morphemes but not other basic aspects of language production or comprehension. These findings are intriguing because they raise important questions about the functional architecture of language processing, including critically, the relationship between production and comprehension. Here, we highlight some of the puzzles that remain and that we hope will guide future empirical explorations of the cognitive and neural mechanisms that support our capacity for language. © 2018 IBRO. Published by Elsevier Ltd. All rights reserved.

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The high-level language brain network – which supports aspects of language post perceptual processing and prior to motor output – spans extensive parts of left frontal and temporal lobes (Fedorenko et al., 2010). These regions are selective for language relative to non-linguistic cognitive processes (Fedorenko and Varley, 2016), and they are spatially and functionally distinct from the perceptual and motor language areas. However, *the internal architecture of the high-level language network remains hotly debated*. In particular, is there a meaningful way to functionally divide this network into component parts? And if so, how is linguistic labor shared across those parts in space and time?

Most proposals of the neural architecture of language (Hickok and Poeppel, 2007; Price, 2010; Friederici, 2011; Indefrey, 2011; Hagoort, 2013; Duffau et al., 2014; Fig. 1) assume organization in terms of size and complexity of the relevant linguistic units (sounds vs. words vs. phrases/sentences) and/or types of computations (e.g., phonological processing vs. lexical access vs. syntactic structure building vs. semantic composition). However, these proposals differ both in how they spatially carve up the network into regions, and the cognitive interpreta-

tion they assign to the different regions and white matter tracts, with seemingly no consensus in sight.

Lee et al.'s results bring to the forefront *three issues/questions* that are core to our understanding of how language processing is implemented in the mind and brain, and that deserve further research and discussion in order to bring the field closer to a mechanistic-level understanding of linguistic computations and to distinguish among the competing proposals of the language architecture:

1. *Spatial specificity (characterizes cognitive functions): Are linguistic representations and computations implemented in a spatially (regionally) specific manner? (Fig. 2).*
2. *Functional specificity (characterizes neural units, from individual cells to brain regions): Is each relevant unit functionally specialized for a particular linguistic function? (Fig. 2).*
3. *Comprehension/production overlap: The perceptual and motor machinery aside, do the same brain regions support comprehension and production?*

Most current proposals of the neural architecture of language (Hickok and Poeppel, 2007; Price, 2010; Friederici, 2011; Indefrey, 2011; Hagoort, 2013; Duffau et al., 2014) postulate a distinction between lexico-semantic processing (knowledge and access of word

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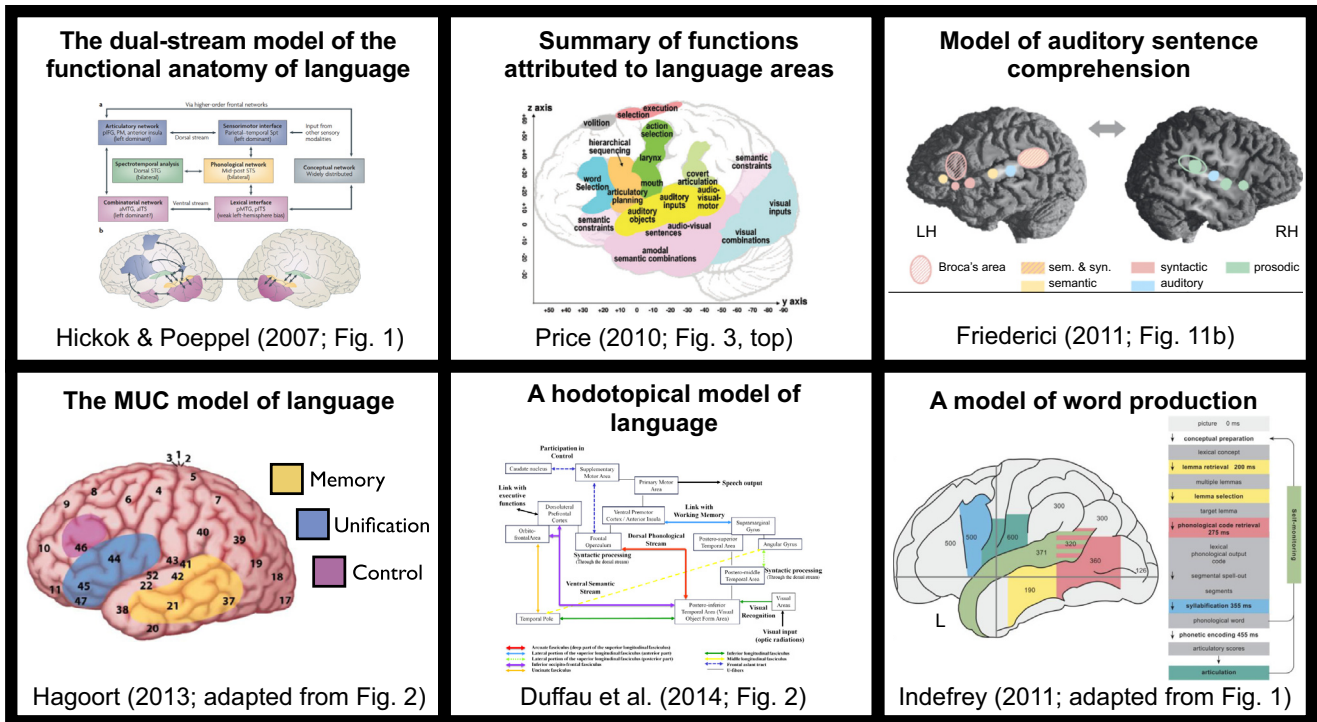


Fig. 1. Some of the leading proposals of the neural architecture of language (Hickok and Poeppel, 2007; Price, 2010; Friederici, 2011; Indefrey, 2011; Hagoort, 2013; Duffau et al., 2014).

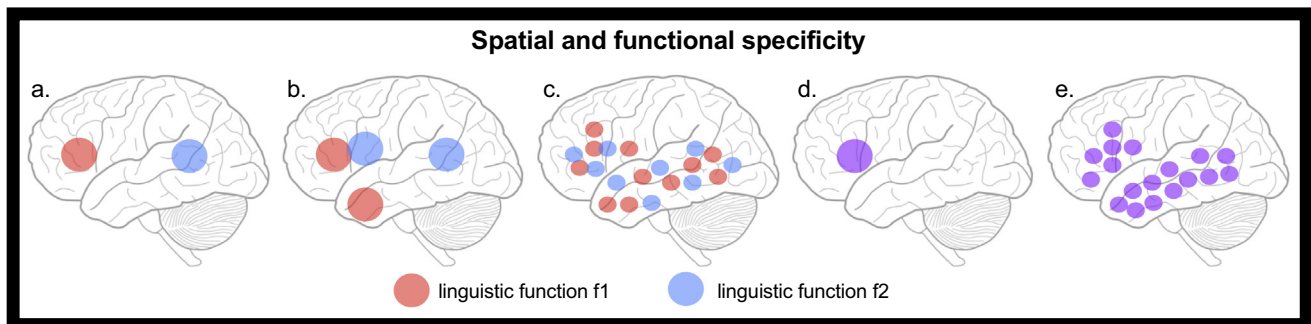


Fig. 2. Illustration of the concepts of spatial and functional specificity. (a) The two linguistic functions are implemented in a spatially specific manner; each relevant brain region is functionally specialized for its function. (b) The two linguistic functions are each implemented across multiple regions; each relevant region is functionally specialized. (c) The two linguistic functions are implemented in a spatially distributed manner across the language cortex without clustering into regions; each cell/voxel/voxel cluster is functionally specialized. (d) The two linguistic functions are implemented in a spatially specific manner; the relevant region performs both functions. (e) The two linguistic functions are implemented in a spatially distributed manner across the language cortex. Each cell/voxel/voxel cluster performs both functions.

meanings) and syntactic/combinatorial processing (knowledge of constraints on combining words into phrases and sentences, and inferring or constructing inter-word dependencies during comprehension and production, respectively). Further, most argue for both spatial and functional specificity of these processes. Many have suggested that syntactic processing is localized to parts of Broca's area (Friederici, 2011; Hagoort, 2013) with the implication that other parts of the network do not support syntactic processing (spatial specificity). Some have further suggested that syntax-responsive areas are *selective* for syntactic over lexico-semantic processing (functional specificity), and that some other language areas

are selective for lexico-semantic processing (Friederici, 2011).

However, much of the evidence for this distinction suffers from methodological limitations (Nieuwenhuis et al., 2011) and a number of neuroimaging and patient studies have failed to observe a dissociation between lexico-semantic and syntactic processing (Dick et al., 2001; Bautista and Wilson, 2016; Blank et al., 2016), putting into question any proposal that postulates this distinction. Further, Huth et al. (2016), Pereira et al. (2018), and others have reported the ability to decode linguistic meanings from across the language network, suggesting a distributed neural representation of semantics that

spans even regions that have been argued by some to be selective for syntactic processing. Lee et al.'s finding of a *focal area* within pSTG which is argued to be *selective* for the production of functional morphemes over other aspects of language processing appears to be at odds with this allegedly distributed and overlapping lexico-semantic and syntactic processing. However, it is important to consider two issues.

First, most evidence for overlap between and distributed nature of lexico-semantic and syntactic processing comes from studies of language *comprehension*. As Lee et al. (2018) note, even though comprehension draws on a set of linguistic knowledge representations also employed during production – in line with extensive cortical overlap between the two (Menenti et al., 2011) – comprehension and production have distinct goals. In comprehension, we need to infer the intended meaning from the linguistic signal. Abundant evidence now suggests that the representations we extract during comprehension are probabilistic and noisy (Traxler, 2014), with the implication that we do not have to perform every structural computation (as long as the meaning is clear). In contrast, in production, we have to express a target meaning by uttering a specific sequence of words where each word takes a particular morpho-syntactic form, so there is substantially less flexibility/optionality. Given that some of the computational demands of production are not shared with comprehension, some brain regions – beyond the lower-level articulation areas – may be selective for (some aspects of) production. According to Hickok and Poeppel (2007), production and comprehension are supported by distinct white matter tracts. Perhaps some cortical areas connected by these tracts are also selective. If so, we should be able to identify such production-selective areas with fMRI. For example, the area that Lee et al. (2018) have discovered within pSTG should respond during (some) production tasks but not during language comprehension.

And *second*, although Lee et al. (2018) have established some degree of functional specificity of their region, the reported data pattern remains consistent with a number of theoretical possibilities. The narrowest hypothesis – the one Lee et al. (2018) argue for – is that the region in question supports the production of functional morphemes (e.g., the plural marker for nouns: table → table-s, or the past tense marker for verbs: play → play-ed). Progressively broader hypotheses include (a) morphological production more generally, including derivational morphology (e.g., forming nouns from adjectives: happy → happi-ness, or verbs from nouns: vapor → vapor-ize); (b) syntactic production more generally, including the ordering of words; or even (c) general context-dependent word/word-form selection, spanning both syntactic and lexico-semantic contextual constraints. The lexical condition in Lee et al. (2018) could be argued to rule out the latter possibility, but the linguistic context in that condition (e.g., “This is a . . .” followed by a picture) does not strongly constrain the target word, and the task does not even require participants to process the context (they can just name the picture). It is possible that context-dependent, but not context-independent, lex-

ical selection requires the target region within pSTG (e.g., being able to complete lexico-semantically constraining sentences like “I was hungry, so I ate a . . .”). Rigorous testing of task and stimulus contrasts targeting these different components of language will be critical in order to understand the precise functional scope of the region that Lee et al. (2018) report, and to determine how this region fits with other available data from a wealth of methods, paradigms, and linguistic manipulations.

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