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Functional Anatomic Models of Language: Assembling the Pieces

DORIT BEN SHALOM and DAVID POEPPEL

In the past few years, a series of influential review articles have summarized the state of the art with respect to cortical models of language organization. The present article is a mini-review and conceptual meta-analysis of several of the most prominent recent contributions. Based on the models, the authors extract some generalizations to arrive at a more robust model that 1) does justice to the range of neurological data, 2) is more connected to research in linguistics and psycholinguistics, and 3) stimulates hypothesis-driven research in this domain. In particular, the article attempts to unify a few of the current large-scale models of the functional neuroanatomy of language in a more principled manner. First, the authors argue that the relevant type of processing in a given cortical area, that is, memorizing (temporal cortex) versus analyzing (parietal versus synthesizing (frontal), lies at the basis of local neuronal structure and function. Second, from an anatomic perspective, more dorsal regions within each of these (temporal, parietal, and frontal) systems specialize more in phonological processing, middle areas in syntactic processing, and more ventral areas in semantic processing. NEUROSCIENTIST 14(1):119–127, 2008. DOI: 10.1177/1073858407305726

Few images in the neurosciences have achieved the iconic status of the classic brain-language model developed in the latter half of the 19th century. Indeed, until recently, most books and articles discussing the neural basis of language had as their visual centerpiece and basis for explanation the well-known image of a left hemisphere, highlighting in the inferior frontal lobe Broca’s area and in the superior temporal lobe Wernicke’s area, connected by a fiber tract (Fig. 1). There are good reasons why this model has achieved such prominence. One is, of course, its historical significance as one of the first major observations in neuropsychology and systems neuroscience, laying the foundation for the principle of functional localization. A second, very impressive feature is the model’s longevity, due to its clinical utility as a heuristic device to classify both lesions and syndromes. Third, and most relevant for the present considerations, the model constitutes one of the first more or less comprehensive accounts of a higher cerebral function. Although in hindsight both the anatomic and linguistic foundations of the Broca-Wernicke-Lichtheim approach seem somewhat naive, the model reflects a very thoughtful attempt at characterizing complex behavior in neuroanatomic terms—it is the first coherent functional anatomic model of language and perhaps of any higher function.

Empirically, this “classic model” of brain and language was based on deficit-lesion correlations. Given the range of new techniques available to study the human brain in vivo, the central tenets are, unsurprisingly, being extensively reevaluated. And although the classic model has been remarkably robust and resilient, it is clearly no longer sufficient (for review, see Cognition vol. 92, 2004, a special issue detailing numerous new approaches and models; a recent edited volume on Broca’s Region by Grodzinsky and Amunts [2006] examines the range of hypotheses on this frontal cortical area). However, the challenges and proposed changes have not been revolutionary; rather, it seems that the development of brain-language models has been evolutionary in the Darwinian sense: descent with modification. In particular, practically all contemporary large-scale models are deeply tied to the presupposition that Broca’s and Wernicke’s areas are essential to language function. We continue to be left-hemisphere imperialists, tied to two principal areas at the core of language processing.

A growing sensitivity to linguistic and psycholinguistic knowledge, paired with the emergence of many new neural recording techniques (fMRI, PET, MEG)—as well as the increasingly sophisticated application of the older ones (EEG, deficit-lesion correlation)—has generated new data on virtually every aspect of language processing, ranging from acoustic phonetics to the semantics of quantification, and the new data have generated new large-scale models. The new models are, of course, increasing in sophistication both anatomically and linguistically. But, we contend, even though these
models are direct descendants of the “classic” view in their attempts to be comprehensive and to find generalizations and explanations holding across a range of language phenomena, they are still—for better or for worse—limiting themselves to restricted domains. It is our goal to compare some of the models’ key attributes, identify some organizing principles, and propose two integrative hypotheses that serve to develop a more unified view of the new functional anatomy of language.

We focus here on several recent contributions that have synthesized impressive amounts of data to develop new large-scale models. In particular, we discuss the models outlined by Price (2000), Friederici (2002), Hickok and Poeppel (2004), and Indefrey and Levelt (2004). (For a comprehensive and thoughtful recent review, primarily of the contribution of neuroimaging, we recommend Demonet and others [2005]. For up-to-date reviews that focus on the cortical organization of speech processing per se, the reader may wish to consider Davis and Johnsrude [2007] and Hickok and Poeppel [2007].) We briefly summarize what we take to be the salient properties of each model, as well as the principal limitations. Subsequently, we attempt to integrate across these proposals by outlining some principles that predict which cortical areas will be implicated in language processing of a certain type.

The models, we argue, make functional anatomic commitments to a large-scale architecture for language processing but base their proposals on restricted domains. One model focuses explicitly on lexical level processing (Price 2000), another on combining across items to build linguistics structures (“synthesizing”) (Friederici 2002), a third derives functional anatomic models based primarily on speech perception and analysis of lexical items (Hickok and Poeppel 2000, 2004, 2007), and one is centered on production (Indefrey and Levelt 2004). We suggest that one organizing principle—retrieval of stored forms (“memorizing”) versus considering internal parts of a representation (“analyzing”) versus combining pieces (“synthesizing”)—can both unify our understanding of these models and serve to generate hypotheses and predictions about functional anatomy and the computations associated with the anatomic regions.

In part, our endeavor is driven by “vision envy.” Research on vision has progressed such that we now have consensus on many aspects of the functional organization of visual analysis and recognition. And, in analogy to the classic model and its iconic status, vision research has its own iconic heavyweight: the map of the primate visual system developed by van Essen and colleagues (e.g., Felleman and van Essen 1991). But unlike the language models, the concurrent and hierarchical visual architecture illustrated by

Fig. 1. The “classic model,” following Geschwind 1979, illustrating Broca’s area in the left posterior inferior frontal lobe (historically implicated in language production), Wernicke’s area in the posterior superior temporal lobe (implicated in language comprehension), and the fiber tract that connects them, the arcuate fasciculus. Although the model has been clinically very useful, it must be acknowledged that it is rather underspecified both anatomically and psycholinguistically.
Felleman and van Essen is connected in detail to neuroanatomic, neurophysiological, and computational proposals, and it has perceptual interpretations. Although work on the human cortex cannot (yet) attain the level of anatomic and physiological detail possible in nonhuman primate studies of the visual system, there is no reason why we cannot be more explicit in computational terms. The granularity of analysis typical of neurolinguistics is still far too coarse. We could and should learn from computational neuroscience and how it has enriched models of vision attempting to be comprehensive. Whereas we are not yet poised to suggest similarly detailed models, it seems necessary and useful to begin to formulate hypotheses that allow more computationally motivated models to be constructed.

The Models

The Broca-Wernicke-Lichtheim-Geschwind model (the classic model) was the first large-scale functional anatomical proposal on language processing (see Fig. 1). It was the result of the cumulative efforts of Broca, Wernicke, and Lichtheim during the 19th century, together with a modern revival incorporating one major modification by Geschwind (1967). Broca’s main discovery, originally reported in 1861 and widely described and reviewed in the literature (Caplan 1987; Stemmer and others 1997; Hagoort and Brown 2001; for some historical predecessors, see Bouillaud 1825 and Dax 1863), was that a patient who had been unable to pronounce anything but one syllable (“tan”) was discovered, upon a postmortem analysis, to have had a large lesion in his left inferior frontal cortex. Based on this correlation, Broca concluded that part of the second or third convolutions of the left inferior frontal gyrus has a necessary role in speech production, or what he, and Bouillaud before him, called the faculty of spoken language. Similarly, Wernicke (1874) observed that lesions in the posterior aspect of the superior temporal gyrus were correlated with fluent but nonsensical language production as well as impaired comprehension, perhaps as a result of impaired auditory feedback. Wernicke concluded that this part of the posterior superior temporal gyrus has a necessary role in speech perception. Lichtheim (1885) synthesized these two claims, positing in addition a “connecting” conceptual area to yield a three-component functional neuroanatomical model of language: Language perception was assumed to implicate Wernicke’s area, language production Broca’s area, and (diffuse) connecting regions were assumed to be responsible for semantic processing. This generated the famous “house” scheme, a model that is alive and well and at the core of many (perhaps still most) textbook discussions of the neural basis of language. Geschwind (1967) adopted most of the assumptions of Lichtheim’s original formulation but suggested that semantic processing has a localized substrate as well, probably involving the inferior parietal cortex.

One major advantage of the Broca-Wernicke-Lichtheim-Geschwind model is simply that it was the first of its kind. Another, more substantive, advantage is that its main predictions, including the roles of Broca’s area, Wernicke’s area, and the inferior parietal cortex, still serve as useful heuristics despite numerous extensions and modifications. Clinical practice has been guided by the central tenets of this model for decades, suggesting that in broad terms, the model has captured essential aspects of patient performance. In hindsight, the model’s main disadvantages are 1) its anatomic underspecification (too few areas are implicated; the implicated areas are interpreted in too monolithic a manner) and 2) its linguistic underspecification. With regard to the latter issue, the model’s restriction to word-level language phenomena precludes any systematic and principled discussion of syntactic processing or any aspects of the compositionality of language.

One of the modern descendants of the classic model is that of Price (2000) (Fig. 2). Reconciling neuropsychological and neuroimaging data as well as cognitive psychological proposals, Price suggests a model of language processing according to which acoustic analysis of words is conducted in the superior temporal cortex, visual analysis of words in the posterior inferior temporal cortex and temporo-occipital cortex, and semantic representation in a network that includes the angular gyrus and the anterior inferior temporal cortex. In this model, there are two routes to phonological-lexical retrieval: a nonspeech route, through the posterior superior temporal cortex, and a semantic route, through the posterior inferior temporal cortex. Articulatory planning is conducted in the anterior insula and the anterior part of Broca’s area, and motor output is computed by the motor cortex.

The model is consistent with classic models of language in that acoustic-phonetic analysis of words is conducted in the posterior superior temporal cortex, although Price suggests that the exact location of this analysis is the superior temporal sulcus rather than the superior temporal gyrus. Similarly, it suggests that the role traditionally played by Broca’s area in articulatory planning of speech is conducted by the anterior insula rather than the neighboring anterior Broca’s area itself, a point that converges with lesion analysis data published by Dronkers (1996).

One main advantage of Price’s (2000) model is its emphasis on semantic processing, especially as it highlights the involvement of the parietal angular gyrus and the anterior inferior temporal cortex. Its main limitation is the exclusive emphasis on word-level semantics, precluding the possibility of capturing any compositional semantics. In that sense, the model is very closely linked to the classic account.

Friederici explicitly departs from the focus on word-level processing. Friederici’s (2002) model makes two major claims. One concerns functional anatomy: the temporal lobes are argued to subserve aspects of syntactic and semantic identification, that is, the retrieval of memorized forms of syntactic and semantic items, whereas frontal regions are argued to subserve the construction of syntactic and semantic relations. The other claim addresses the order of and interaction between syntactic and semantic processes. It is argued that initial syntactic structure building precedes, and in many respects independent of, semantic processing. Syntactic and semantic processes may interact, however, during
on an analogy between the visual and the auditory processing streams. It is well established that the visual stream contains at least two substreams: a ventral stream, projecting principally to the temporal lobe and responsible for visual object recognition (the so-called what stream), and a dorsal stream, projecting to the parietal and frontal lobes and involved in the visual representation of spatial attributes (the so-called where stream) (Mishkin and Ungerleider 1982). A more recent perspective stresses that the dorsal where stream is an important interface between visual and motor processing in the brain (Milner and Goodale 1995). According to Hickok and Poeppel (2004), the auditory stream for language processing is similarly organized: A ventral stream (which itself is extensively subdivided; see Hickok and Poeppel 2007), projecting to various temporal lobe regions, is involved with auditory recognition. A dorsal stream, projecting from the core auditory cortex to the parietal and frontal lobes, is the interface between auditory and motor processing. This last point is especially important in the context of language processing, offering a potential resolution to a long-standing open question, namely, the dual nature of distinctive features (the smallest units of spoken language and lexical representation) as both auditory- and motor- (articulatory) units (cf. the motor theory of speech perception; Liberman and Mattingly 1985).

In terms of the classic language areas (Broca’s, Wernicke’s), the model proposed by Hickok and Poeppel has little computationally explicit to say about the frontal lobe, including Broca’s area (although given its role in articulation, it is assumed that it does interact with the dorsal auditory stream). Wernicke’s area is discussed, comparable to other recent proposals, as encompassing a temporal area—here assumed to be part of the auditory ventral stream—and a temporoparietal area—here assumed to be part of the auditory-motor interface of the auditory dorsal stream.

A main advantage of Hickok and Poeppel’s model is its unifying treatment of the dual nature (auditory/motor) of speech representations. A major disadvantage is its inability to make direct predictions about the role of frontal areas, including the left inferior frontal gyrus, and Broca’s area, in particular. However, given the extensive involvement of Broca’s area in phonological processing (see Burton 2001, for review), it stands to reason that Broca’s area (specifically some part of Broca’s area, which must be further subdivided; see Grodzinsky and Amunts 2006) can and must be discussed in terms of computations that underlie the analysis of the phonological representations of single items.

Finally, Indefrey and Levelt (2004) (Fig. 4) base their functional anatomy on a model of word production. According to this model, word production (as elicited by, say, picture naming) involves five main types of representations: a lexical concept (generated approximately 175 ms after stimulus presentation); a target lemma (about 250 ms after stimulus presentation); a lexical phonological output code, which is then spelled out into segments (around 330 ms); a syllabified phonological output (around 455 ms); and, finally, an articulatory score (around 600 ms). Anatomically, this translates into later stages of language processing. Based on extensive electrophysiological work, Friederici identifies three responses that are argued to reflect sentence processing stages, including the ELAN and LAN responses (indicative of early syntactic structure building), the N400 response that relates to lexical-semantic processing, and the P600 response that correlates with repair and reanalysis processes.

Friederici (2002) makes explicit claims regarding the roles of the classic language areas. Based on studies showing activation of Broca’s area in various tasks, including processing musical sequences (Maess and others 2001), perceiving the rhythm of motion (Schubotz and von Cramon 2001), and perceiving the imagery of motion (Binkofski and others 2000), it is argued that Broca’s area is involved in processing both language and nonlanguage sequences, and not just language syntax as traditionally assumed (see Poeppel and Embick 2006, for some discussion). As for Wernicke’s area, given that parietal regions are not part of Friederici’s model, only the posterior superior temporal cortex is considered, and it is assumed to have a fairly traditional role, that is, the identification of (phonological) word form.

The two main advantages of Friederici’s (2002) model are 1) the distinction it draws between the identification of word-level syntactic and semantic information in the temporal lobe and syntactic and semantic relation-building in the frontal lobe and 2) its sophisticated treatment of the nature of the interaction between syntactic and semantic processing. Its main disadvantage is that the model does not incorporate the contributions of parietal areas.

Hickok and Poeppel (2004) (Fig. 3) approach the problem from a very different angle, motivated in large part by questions about speech perception. They build into

Fig. 2. Following Price (2000). Acoustic analysis of words is carried out in the superior temporal cortex, and visual analysis of words in the posterior inferior temporal cortex and temporo-occipital cortex. Crucially, the semantic representation of linguistic input is computed in a network that includes the angular gyrus and the anterior inferior temporal cortex.

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lemma retrieval and selection in the middle temporal gyrus, phonological code retrieval in the posterior middle and superior temporal gyrus, syllabification in the posterior inferior frontal cortex, and articulation in the inferior precentral and postcentral gyrus. In terms of its proposal about the temporal lobe, this model converges with the hypotheses articulated in Hickok and Poeppel (2004); this suggests that perception and production data at the single-word level of analysis yield comparable functional anatomic assignments.

In terms of the classic language areas, Indefrey and Levelt’s (2004) model agrees that Wernicke’s area (the posterior superior temporal gyrus) is involved in the lexical auditory representation of words, even though it suggests that the posterior middle temporal lobe is also involved in phonological code retrieval, at least during production. As for Broca’s area, the model agrees that it has a role in the phonological production of words, specifically in the concatenation of syllables as the last step before phonetic encoding.

Two main advantages of the Indefrey and Levelt (2004) model are that it is based on a detailed psycholinguistic model of word production, on one hand, and a meticulous meta-analysis of 82 word production experiments, on the other. It is also the only model among those reviewed here that correlates the processing of lexical syntactic features with an anatomical region (the midportion of the middle temporal cortex). Its two main disadvantages are its relative focus on language production and its exclusion of almost all parietal regions, probably because its authors excluded studies involving either semantic or phonological decisions (such as phonemic or semantic monitoring).

**A Hypothesis about Unification**

In summary, these models capture, more or less successfully, large-scale functional anatomies but are limited to a narrow scope of processing. The idea we outline in this article attempts to synthesize critical elements of these proposals and describes the functional neuroanatomy of language processing in terms of the intersection of three different aspects of language processing, namely, phonological, syntactic, and semantic processing, and three different types of operations underlying various aspects of language processing, namely, memorizing (or, given the emphasis on adult language processing, retrieval of stored items), analyzing, and synthesizing (combinatory) processes. To be sure, our proposal is a modest one. Whereas an ultimate goal is to develop a theoretically motivated, computationally explicit, and biologically sensible model for the functional anatomy of language, here we merely strive to find some convergence and overlap across a few models to generate some hypotheses about the possible representations and computations that are associated with different parts of the network.

**Frontal Lobe**

One first step concerns the increased anatomic specification of these areas. Based on a meta-analysis of functional neuroimaging studies, Bookheimer (2002) suggests that...
the left inferior frontal cortex can be divided up into three
different territories: a more dorsal area—the superior pos-
terior region of the inferior frontal cortex (Brodmann areas
44/6); a middle area—the central mid–inferior frontal cor-
tex (Brodmann areas 45/44); and a more inferior area—
the inferior anterior inferior frontal cortex (Brodmann
areas 47/45). This subdivision is at least in part supported
by recent anatomic work (see, e.g., papers in Grodzinsky
and Amunts 2006). According to Bookheimer’s analysis,
the most superior of these areas specializes in phonologi-
cal processing, the midregion in syntactic processing, and
the most inferior in semantic processing (see also Burton
2001; Hagoort 2005; Thompson-Schill 2005 for argu-
ments supporting this division). Importantly for present
purposes, Bookheimer argues that most of the processing
done by these frontal regions are about combining pieces,
creating relations that can span different words. This means
assembling syllables, within and between words, thus effec-
tively synthesizing phonological information (in the case of
the more superior region), computing the syntactic relation-
ships between different words (in the case of the middle
region), and processing semantic relationships between dif-
ferent words (in the more inferior region). Because of the
absolute requirement that any satisfactory model account for
combinatorics and compositionality somehow and some-
where, it is reasonable to hypothesize that these operations
are mediated in these frontal areas. Whether the elemental
representations in play are phonological (distinctive fea-
tures, syllables) and subject to concatenation, or hierarchical
and subject to syntactic organization, or conceptual and sub-
ject to semantic composition, the three left frontal areas are
plausibly implicated in these synthesizing operations.

What was traditionally known as Broca’s area, then (BA
44/45 and possibly incorporating the frontal operculum), is
combined with the regions immediately anterior and infe-
rior to it (this is supported by recent connectivity data by
Anwander and others 2007), and this entire region is
divided into three distinct parts: The most superior is
involved in some of the phonological operations. The
middle section performs some of the more syntactic com-
putations. The most inferior area is engaged in semantic
processing. All three areas are involved in synthesizing
information between elementary (phonological, lexical,
semantic) items. What is not clear is how to characterize
these computations such that they can also plausibly cap-
ture the many nonlinguistic tasks that have activated
Broca’s area (see, for example, Embick and Poeppel
2006, for a brief summary). Such data suggest that the
computations are likely to be rather abstract (and in some
sense “generic”), attaining their putative specificity for
language by virtue of the representations that enter into
the computations mediated therein.

Temporal Lobe

Recent evidence also implicates various parts of the tem-
poral lobe in lexical phonological, semantic, and syntactic
processing. There is by now consensus that the temporal
region associated with Wernicke’s area (the superior pos-
terior temporal cortex) is involved in processing phono-
logical representations of single words (perhaps through
the mechanism of a template-matching algorithm; Warren
and others 2005). For example, Friederici (2002) argues
that the superior posterior temporal cortex is responsible
for the identification of phonological word form. This is, in
a sense, a modern descendant of Wernicke’s original idea
that the superior posterior temporal cortex is responsible
for the “auditory images of words.” In a similar vein,
Hickok and Poeppel (2000, 2004) argue 1) that superior
aspects of the temporal lobe are the origin of the dual
(ventral and dorsal) streams mediating speech perception,
2) that the superior temporal lobe (bilaterally) performs
acoustic-phonetic mapping, and 3) that the inferior tem-
poral lobe is implicated in the mapping from sound to
meaning. One piece of evidence for the involvement of the
posterior superior temporal gyrus in the output phonologi-
cal form of single words comes from the work of Anderson
and others (1999).

Price (2000) emphasizes the role of the inferior anterior
temporal cortex in semantic processing, a hypothesis that
is supported by evidence both from lesions and from func-
tional imaging studies. For example, the inferior temporal
lobe has been reliably linked to some aspects of the N400,
the most famous ERP component associated with seman-
tic processing: Data gathered using depth electrodes
(McCarthy and others 1995), fMRI, and ERP (Rossell and
others 2003) all support this claim. In addition, there is
some evidence from lesion studies that atrophy in the infe-
rior anterior temporal cortex can lead to a profound loss of
semantic knowledge (e.g., Ikeda and others 2006).

Moreover, as Friederici (2002) points out, there is reason
to believe that the contribution of the temporal cortex to
semantic processing is in terms of the processing of lexical
semantics, that is, semantic processing of single words.
With respect to syntactic processing, the extensive meta-analysis by Indefrey and Levelt (2004) has suggested that the selection of word-level syntactic information (e.g., word-level syntactic category) involves the mid middle temporal cortex. Again, consistent with Friederici (2002), it seems that the temporal cortex subserves the retrieval of word-level syntactic information, whereas the frontal cortex is involved in coordinating relations between basic items (primitives).

Thus, there is some evidence for a dorsal-to-ventral gradient in the temporal lobe, too, with the more dorsal regions subserving phonological processing, middle areas morpho-syntactic processing, and ventral areas retrieval of (lexical) semantic representations (e.g., Damasio and others 2004).

Parietal Lobe
Price (2000) suggests that the angular gyrus (inferior ventral parietal cortex) is involved in semantic processing. This claim is supported by neuroimaging and studies of deficit-lesion patterns. Patients with damage to the left angular gyrus have comprehension deficits in both written and spoken language (e.g., Hart and Gordon 1990), and fMRI data implicate the angular gyrus in some aspects of semantic processing (e.g., Baumgaertner and others 2002). In particular, a study by Price and others (1997) compared conscious semantic and phonological decision tasks. The angular gyrus was activated more during conscious semantic decision making (e.g., does an item denote a living or a nonliving concept), which requires the analysis of sublexical-semantic information.

Similarly, the supramarginal gyrus (superior ventral parietal cortex) was activated in the reverse contrast, that is, more during conscious phonological decision making (e.g., does an item have two syllables or does it not), which requires the analysis of sublexical-phonological information. More generally, and consistent with Hickok and Poeppel (2004), this area seems to be necessary for sublexical acoustic-phonemic processing (e.g., Caplan and others 1995). In addition, in terms of both location and function, this area may correspond to area Spt identified by Hickok and others (2003), which is argued to be involved in phonological working memory. For example, area Spt is a little posterior to the closely related ventral inferior parietal area discussed by Ravizza and others (2004) as being involved in phonological encoding-recoding.

More tentatively, extending the patterns in the frontal and temporal lobes, one could predict that an area in the middle ventral parietal lobe (between the angular gyrus and the supramarginal gyrus) would show activation during morphological analysis. A careful recent study of morphological derivation showed increased brain activation during verb derivation versus verb repetition and adjective derivation versus adjective repetition in left parietal regions including the angular and supramarginal gyri (Marangolo and others 2006) (Fig. 5).

Summary
This article suggests a model of the functional neuroanatomy of language processing that is consistent with a large body of available evidence. The data suggest, first, that the lobes differ in terms of their type of language analysis: memorizing (learning new and retrieving stored primitives) in the temporal lobe, analyzing (accessing subparts of stored items) in the parietal lobe, and synthesizing (creating combinations of stored representations) in the
frontal lobe. The basic items (or primitives, or ontological constituents—or more colloquially, the “parts list”) naturally differ for different levels of analysis (phonology, morphology, syntax, semantics). For a specification of the primitives as well as hypotheses as to precisely how they combine to yield linguistic representations, we look to linguistic and psycholinguistic research. The data suggest, second, that a common anatomic pattern in the inferior parietal lobe, the inferior frontal lobe, and the entire temporal lobe is that dorsal areas are involved in phonological processing, middle areas in morpho-syntactic processing, and inferior areas in semantic processing (compare our view to similar claims arguing for the similarities/distinctions between the role of the posterior aspect of the superior temporal gyrus and the more superior part of the inferior frontal cortex in phonological processing, and the role of the anterior and posterior inferior temporal cortex and the more ventral aspect of the inferior frontal cortex in semantic processing; Crinion and others 2003; Rodd and others 2005). Whereas the anatomical data simply constitute a descriptive generalization about some of the findings, the hypothesis about which types of analysis are systematically implicated may lead to the formulation of some computational hypotheses about how the pieces—the units of linguistic representation and processing—are assembled.

There are, to be sure, clear advantages to making anatomical specifications. For one, in conjunction with a sophisticated task analysis, anatomic hypotheses help generate detailed predictions for functional imaging and lesion studies, according to both linguistic content and type of linguistic analysis. For example, processing of syntactic and semantic lexical aspects of, say, nominal gender is predicted to involve activation in the temporal lobe, but the activation associated with the semantic processing is predicted to be more inferior. In addition, specific anatomic hypotheses might help relate general characteristics of the frontal, temporal, and parietal lobes to their putative roles in linguistic representation and processing—are assembled.

References
Bouillaud JB. 1825. Recherches cliniques propres à démontrer que la perte de la parole correspond à la lésion des lobules antérieurs du cerveau. Archives Générales de Médecine 8:25–45.