

The Neuroscientist

<http://nro.sagepub.com>

Functional Anatomic Models of Language: Assembling the Pieces

Dorit Ben Shalom and David Poeppel

Neuroscientist 2008; 14; 119 originally published online Oct 2, 2007;

DOI: 10.1177/1073858407305726

The online version of this article can be found at:
<http://nro.sagepub.com/cgi/content/abstract/14/1/119>

Published by:



<http://www.sagepublications.com>

Additional services and information for *The Neuroscientist* can be found at:

Email Alerts: <http://nro.sagepub.com/cgi/alerts>

Subscriptions: <http://nro.sagepub.com/subscriptions>

Reprints: <http://www.sagepub.com/journalsReprints.nav>

Permissions: <http://www.sagepub.com/journalsPermissions.nav>

Citations <http://nro.sagepub.com/cgi/content/refs/14/1/119>

Functional Anatomic Models of Language: Assembling the Pieces

DORIT BEN SHALOM and DAVID POEPEL

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

KEY WORDS *Language, Anatomy, Temporal, Parietal, Frontal*

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

From the Department of Foreign Literatures and Linguistics, Zlotowski Center for Neuroscience, Ben Gurion University of the Negev, Beer-Sheva, Israel (DBS), and Department of Linguistics, Department of Biology, Cognitive Neuroscience of Language Laboratory, University of Maryland, College Park, MD (DP).

DB was partially supported by the Israeli Science Foundation. DP is supported by NIH R01 DC 05660. The authors thank Susannah Hofmann for her excellent support in preparing this article.

Address correspondence to: Dorit Ben Shalom, Department of Foreign Literatures and Linguistics, Zlotowski Center for Neuroscience, Ben Gurion University of the Negev, P.O. Box 653, Beer-Sheva 84105, Israel (e-mail: doritb@bgu.ac.il).

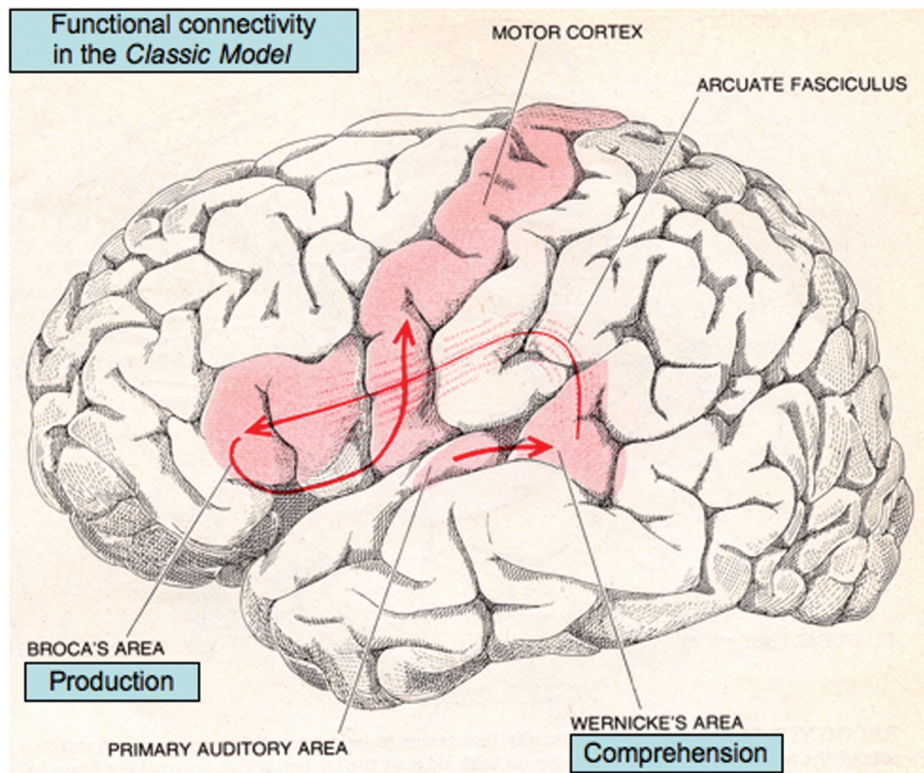


Fig. 1. The “classic model,” following Geschwind 1979, illustrating Broca’s area in the left posterior inferior frontal lobe (historically implicated in language production), Wernicke’s area in the posterior superior temporal lobe (implicated in language comprehension), and the fiber tract that connects 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.

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 Johnsruide [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

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 nonsemantic 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 is in many respects independent of, semantic processing. Syntactic and semantic processes may interact, however, during

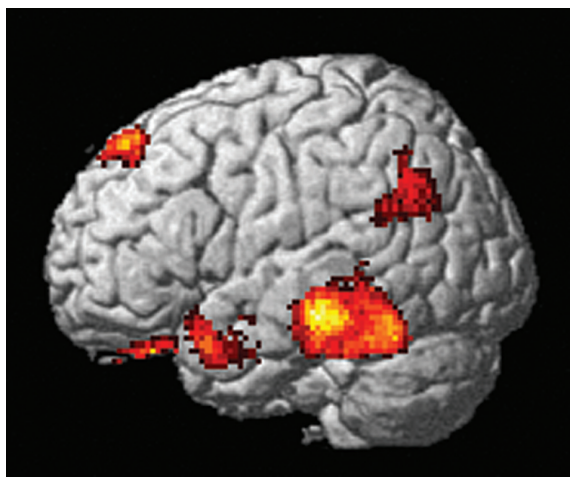


Fig. 2. Following Price (2000). Acoustic analysis of words is carried out in the superior temporal cortex, and visual analysis of words in the posterior inferior temporal cortex and temporo-occipital cortex. Crucially, the *semantic* representation of linguistic input is computed in a network that includes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

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 sublexical-phonological units and/or 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

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

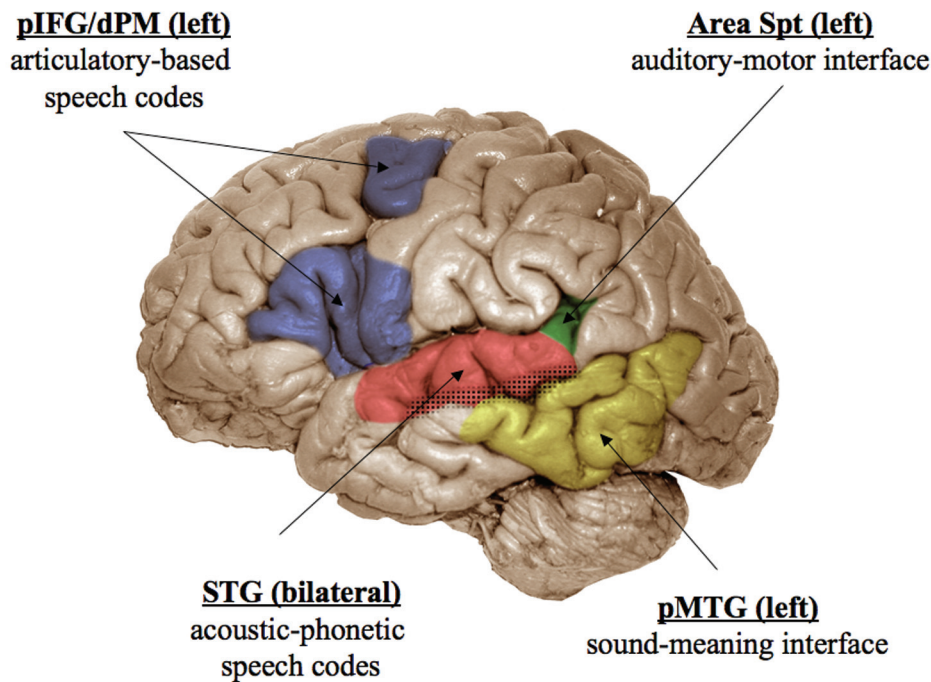


Fig. 3. From Hickok and Poeppel (2004). A ventral auditory stream, projecting to various temporal lobe regions, is involved with auditory recognition. A dorsal stream, projecting from the core auditory cortex to the parietal and frontal lobes, is the interface between auditory and motor processing. pIFG = posterior inferior frontal gyrus; dPM = dorsal premotor cortex; STG = superior temporal gyrus; pMTG = posterior middle temporal gyrus.

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

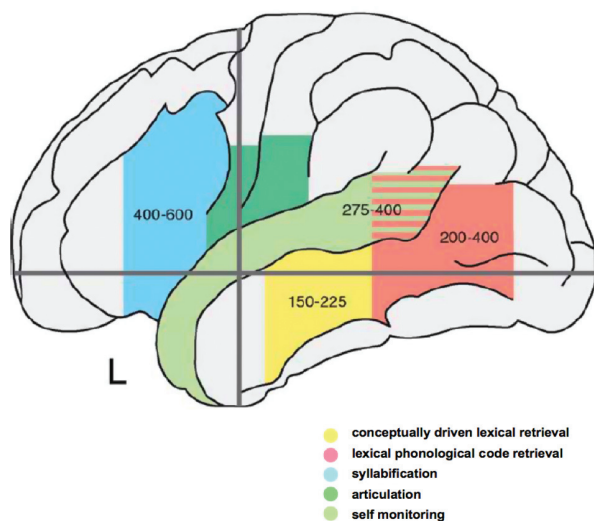


Fig. 4. From Indefrey and Levelt (2004). Lemma retrieval and selection are argued to occur in the middle temporal gyrus, phonological code retrieval in the posterior middle and superior temporal gyrus, syllabification in the posterior inferior frontal cortex, and articulation in the inferior pre-central and postcentral gyri.

the left inferior frontal cortex can be divided up into three different territories: a more dorsal area—the superior posterior region of the inferior frontal cortex (Brodmann areas 44/6); a middle area—the central mid–inferior frontal cortex (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 phonological processing, the midregion in syntactic processing, and the most inferior in semantic processing (see also Burton 2001; Hagoort 2005; Thompson-Schill 2005 for arguments 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 effectively synthesizing phonological information (in the case of the more superior region), computing the syntactic relationships between different words (in the case of the middle region), and processing semantic relationships between different words (in the more inferior region). Because of the absolute requirement that any satisfactory model account for combinatorics and compositionality somehow and somewhere, it is reasonable to hypothesize that these operations are mediated in these frontal areas. Whether the elemental representations in play are phonological (distinctive features, syllables) and subject to concatenation, or hierarchical and subject to syntactic organization, or conceptual and subject 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 inferior 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 computations. 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 capture 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 temporal lobe in *lexical* phonological, semantic, and syntactic processing. There is by now consensus that the temporal region associated with Wernicke’s area (the superior posterior temporal cortex) is involved in processing phonological 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 temporal 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* phonological 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 functional 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 semantic 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 inferior 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.

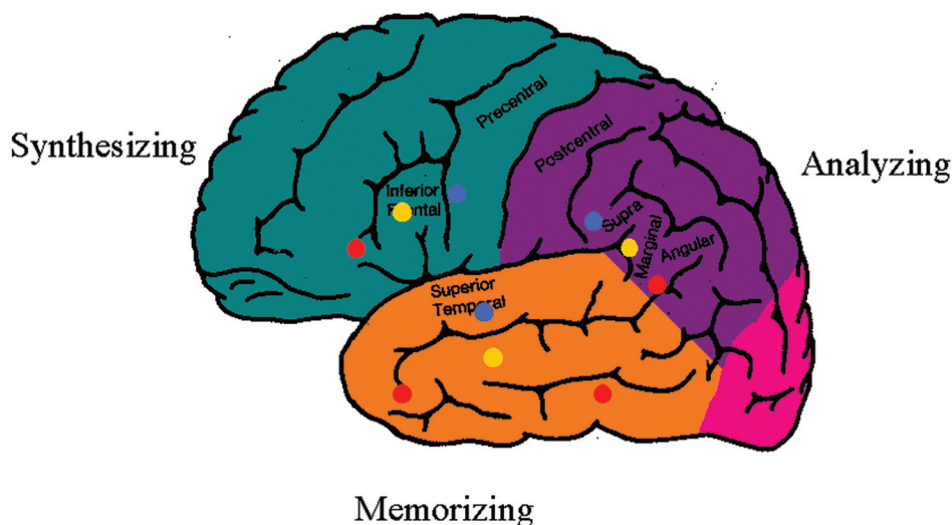


Fig. 5. Two organizing principles, derived from the literature, are made explicit in this summary figure. In our view, the conceptual meta-analysis suggests 1) the temporal lobe deals principally with *memorizing* (storing) lexical items and facilitating their retrieval, the parietal lobe with *analyzing* these items, and the frontal lobe with *synthesizing* the representations. 2) Spatially, there is a superior-to-inferior gradient in each lobe, with phonetic/phonological information being mapped in more superior/dorsal fields, syntactic information in the middle, and semantic representations more inferiorly/ventrally. Blue = sounds; yellow = words; red = meaning.

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 language processing; for example, the well-established specialization of the temporal lobe for memorizing items is commensurate with its putative role in the *storage* of linguistic units, the traditional role of the frontal lobe in motor sequencing with its hypothetical role in the *combination* of linguistic units, or the emerging role of the parietal lobe in the conversion (coordinate transformation) of sensory subunits to motor subunits with its suggested role in the *analysis* of sublexical linguistic units. Cumulatively, a more principled way to think about the mapping of representation to anatomy should allow the formulation of computational hypotheses about the language system of the human brain and permit a more Marrian perspective (Marr 1982) on the cognitive neuroscience of language that incorporates computational, algorithmic, and implementational approaches.

References

- Anderson JM, Gilmore R, Roper S, Crosson B, Bauer RM, and others. 1999. Conduction aphasia and the arcuate fasciculus: a reexamination of the Wernicke-Geschwind model. *Brain Language* 70:1–12.
- Anwander A, Tittgemeyer M, von Cramon DY, Friederici AD, Knösche TR. 2007. Connectivity-based parcellation of Broca’s area. *Cereb Cortex* 17:816–25.
- Baumgaertner A, Weiller C, Büchel C. 2002. Event-related fMRI reveals cortical sites involved in contextual sentence integration. *Neuroimage* 16:736–45.
- Binkofski F, Amunts K, Stephan KM. 2000. Broca’s region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum Brain Mapp* 11:273–85.
- Bookheimer S. 2002. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annu Rev Neurosci* 25:151–88.
- Bouillaud JB. 1825. Recherches cliniques propres à démontrer que la perte de la parole correspond à la lésion des lobules antérieures du cerveau. *Archives Générales de Médecine* 8:25–45.
- Broca PP. 1861. Perte de la parole. *Bulletins de la Société Anthropologique de Paris* 2:235–8.
- Burton MW. 2001. The role of inferior frontal cortex in phonological processing. *Cogn Sci* 25:695–709.
- Caplan D. 1987. *Neurolinguistics and linguistic aphasiology: an introduction*. New York: Cambridge University Press.
- Caplan D, Gow D, Makris N. 1995. Analysis of lesions by MRI in stroke patients with acoustic-phonetic processing deficits. *Neurology* 45:293–8.
- Crinion JT, Lambon-Ralph MA, Warburton EA, Howard D, Wise RJS. 2003. Temporal lobe regions engaged during normal speech comprehension. *Brain* 126:1193–201.
- Damasio H, Tranel D, Grabowski T, Adolphs R, Damasio A. 2004. Neural systems behind word and concept retrieval. *Cognition* 92(1-2): 179–229.
- Davis M, Johnsrude I. 2007. Hearing speech sounds: top-down influences on the interface between audition and speech perception. *Hear Res* doi:10.1016/j.heares.2007.01.014.
- Dax G. 1863. Observations tendant à prouver la coincidence constante des dérangements de la parole avec une lésion de l’hémisphère gauche du cerveau. *Comptes Rendus Hebdomadaire des Séances de l’Académie des Sciences* 61:534.
- Demonet JF, Thierry G, Cardebat D. 2005. Renewal of the neurophysiology of language: functional neuroimaging. *Physiol Rev* 85:49–95.
- Dronkers NF. 1996. A new brain region for coordinating speech articulation. *Nature* 384:159–61.
- Embick D, Poeppel D. 2006. Mapping syntax using imaging: prospects and problems for the study of neurolinguistic computation. In: Brown K, editor. *Encyclopedia of language and linguistics*. 2nd ed. Oxford (UK): Elsevier. Vol. 7, p. 484–486.
- Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* 1:1–47.
- Friederici AD. 2002. Towards a neural basis of auditory sentence processing. *Trends Cogn Sci* 6:78–84.
- Geschwind N. 1967. The varieties of naming errors. *Cortex* 3:97–112.
- Geschwind N. 1979. Specialization of the human brain. *Sci Am* 241:180–99.
- Grodzinsky Y, Amunts K. 2006. Broca’s region: mysteries, facts, ideas, and history. New York: Oxford University Press.
- Hagoort P. 2005. On Broca, brain, and binding: a new framework. *Trends Cogn Sci* 9:416–23.
- Hagoort P, Brown CM. 2001. *The neurocognition of language*. New York: Oxford University Press.
- Hart J, Gordon B. 1990. Delineation of single-word semantic comprehension deficits in aphasia, with anatomical correlation. *Ann Neurol* 27:226–31.
- Hickok G, Poeppel D. 2000. Towards a functional neuroanatomy of speech perception. *Trends Cogn Sci* 4:131–8.
- Hickok G, Poeppel D. 2004. Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* 92:67–99.
- Hickok G, Poeppel D. 2007. The cortical organization of speech perception. *Nat Neurosci Rev* 8:393–402.
- Hickok G, Buchsbaum B, Humphries C, Muftuler T. 2003. Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. *J Cogn Neurosci* 15:673–82.
- Ikeda M, Patterson K, Graham KS, Ralph MA, Hodges JR. 2006. A horse of a different colour: do patients with semantic dementia recognise different versions of the same object as the same? *Neuropsychologia* 44:566–75.
- Indefrey P, Levelt WJ. 2004. The spatial and temporal signatures of word production components. *Cognition* 92:101–44.
- Lieberman AM, Mattingly IG. 1985. The motor theory of speech perception revised. *Cognition* 21:1–36.

- Lichtheim L. 1885. On aphasia. *Brain* 7:433–84.
- Maess B, Koelsch S, Gunter TC, Friederici AD. 2001. Musical syntax is processed in Broca's area: an MEG study. *Nat Neurosci* 4:540–5.
- Marangolo P, Piras F, Galati G, Burani C. 2006. Functional anatomy of derivational morphology. *Cortex* 42:1093–106.
- Marr D. 1982. *Vision*. New York: W. H. Freeman.
- McCarthy G, Nobre AC, Bentin S, Spencer DD. 1995. Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *J Neurosci* 15:1080–9.
- Milner AD, Goodale MA. 1995. *The visual brain in action*. New York: Oxford University Press.
- Mishkin M, Ungerleider LG. 1982. Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behav Brain Res* 6:57–77.
- Poeppel D, Embick D. 2005. Defining the relation between linguistics and neuroscience. In: Cutler A, editor. *Twenty-first century psycholinguistics: four cornerstones*. Mahwah (NJ): Lawrence Erlbaum Associates. p 103–18.
- Price CJ. 2000. Functional imaging studies of aphasia. In: Mazziotta JC, Toga AW, Frackowiak RSJ, editors. *Brain mapping: the disorders*. San Diego: Academic Press. p 181–200.
- Price CJ, Moore CJ, Humphreys GW, Wise RJS. 1997. Segregating semantic from phonological processes during reading. *J Cogn Neurosci* 9:727–33.
- Ravizza SM, Delgado MR, Chein JM, Becker JT, Fiez JA. 2004. Functional dissociations within the inferior parietal cortex in verbal working memory. *Neuroimage* 22:562–73.
- Rodd JM, Davis MH, Johnsrude IS. 2005. The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cereb Cortex* 15:1261–9.
- Rossell SL, Price CJ, Nobre AC. 2003. The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia* 41:550–64.
- Schubotz RI, von Cramon DY. 2001. Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cereb Cortex* 11:210–22.
- Stemmer B, Whitaker H, editors. 1997. *Handbook of neurolinguistics*. San Diego: Academic Press.
- Thompson-Schill SL. 2005. Dissecting the language organ: a new look at the role of Broca's area in language processing. In: Cutler A, editor. *Twenty-first century psycholinguistics: four cornerstones*. Mahwah (NJ): Lawrence Erlbaum. p 173–89.
- Warren JE, Wise RJS, Warren JD. 2005. Sounds do-able: auditory-motor transformations and the posterior temporal plane. *Trends Neurosci* 28:636–43.
- Wernicke C. 1874. *Der aphasische symptom-complex*. Breslau: Cohn and Weigert.