

**Broca and Wernicke are Dead,
or Moving Past the Classic Model of Language Neurobiology**

Pascale Tremblay^{1,2} and Anthony Steven Dick³

1. Département de Réadaptation, Faculté de Médecine, Université Laval, Québec City, QC, Canada

2. Centre de Recherche de l'Institut Universitaire en Santé Mentale de Québec, Québec City, QC,
Canada

3. Florida International University, Miami, FL, USA

Corresponding Author:

Anthony Steven Dick

Florida International University

Modesto A. Maidique Campus AHC-4 454

11200 S. W. 8th Street

Miami, FL 33199

Phone: 305-348-4202 | Fax: 305-348-3879

Email: adick@fiu.edu

Abstract

With the advancement of cognitive neuroscience and neuropsychological research, the field of language neurobiology is at a cross-roads with respect to its framing theories. The central thesis of this article is that the major historical framing model, the Classic “Wernicke-Lichtheim-Geschwind” model, and associated terminology, is no longer adequate for contemporary investigations into the neurobiology of language. We argue that the Classic model (1) is based on an outdated brain anatomy; (2) does not adequately represent the distributed connectivity relevant for language, (3) offers a modular and “language centric” perspective, and (4) focuses on cortical structures, for the most part leaving out subcortical regions and relevant connections. To make our case, we discuss the issue of anatomical specificity with a focus on the contemporary usage of the terms “Broca’s and Wernicke’s area”, including results of a survey that was conducted within the language neurobiology community. We demonstrate that there is no consistent anatomical definition of “Broca’s and Wernicke’s Areas”, and propose to replace these terms with more precise anatomical definitions. We illustrate the distributed nature of the language connectome, which extends far beyond the single-pathway notion of *arcuate fasciculus* connectivity established in the Geschwind’s version of the Classic Model. By illustrating the definitional confusion surrounding “Broca’s and Wernicke’s areas”, and the by illustrating the difficulty integrating the emerging literature on perisylvian white matter connectivity into this model, we hope to expose the limits of the model, argue for its obsolescence, and suggest a path forward in defining a replacement.

Keywords: Broca’s area; Wernicke’s area; arcuate fasciculus; language neurobiology; language connectome

1. Introduction

“We are tied down to a language which makes up in obscurity what it lacks in style”

-Tom Stoppard, *Rosencrantz and Guildenstern are Dead*, p. 61

A major theme of Stoppard’s play *Rosencrantz and Guildenstern are Dead* deals with the protagonists’ tendency to move through life without direction, unable to make meaningful progress. Thus, Act II of the play opens with a disagreement between the title characters. Guildenstern confidently declares “I think we can say we made some headway”, to which Rosencrantz, disagreeing, responds “You think so”? Such an argument often plays out in the field of the neurobiology of language. In this paper we sympathize with Rosencrantz’s skepticism and suggest that progress in the field of language neurobiology, though initially bolstered by the development of the first neurobiology of language models, in particular the “Wernicke-Lichtheim-Geschwind model” (i.e., the “Classic model”), is now ready to move beyond this model and its terminology to adopt a more modern and integrative perspective.

To make our case, we first provide a brief overview of the Classic Model and show that its terminology is still in wide use. Next we discuss the issue of anatomical specificity with a focus on the contemporary usage of the terms “Broca’s and Wernicke’s area”, including results of a survey that was conducted within the language neurobiology community. We will argue that there is no consistent definition of “Broca’s and Wernicke’s areas”, and propose that the terms’ usage in contemporary models should be replaced by more precise anatomical definitions. Following this, we undertake a brief review of the major advances in understanding the fiber pathway connectivity of the language network. Here, we argue that the notion that a single fiber pathway, the *arcuate fasciculus*, supports language functions in the human brain is obsolete. Without the two major pillars of the theory—i.e., the regions and their connections—we consider the model to be obsolete, and suggest a path forward in defining a replacement.

In making these arguments, we refer throughout the paper to a short survey that was conducted

online during November and December of 2015 (the survey was approved by the Florida International University Institutional Review Board, IRB-15-0259). The survey was posted online and distributed through the Neurobiology of Language Society newsletter, and through targeted emails to language neurobiology researchers. A total of 159 responses were collected, most of them from PhD-level academics. The majority of the respondents (87%) reported working in an academic setting, and 11% reported working in a clinical or hospital setting (3% reported “Other”). Most (73%) reported holding a PhD; 13% a master’s degree; 9% a medical degree, and 4% a baccalaureate. Respondents worked in a variety of disciplines (speech and language pathology, psychology, biomedical engineering, neurology, linguistics/neurolinguistics), with an average of 9 years of experience ($SD = 8.63$ years; Max = 40 years). For this survey, respondents reported familiarity with the Classic model (94%), and good expertise in neuroanatomy (47% reported “A lot [extensive training and frequent use of neuroanatomy knowledge]”; 29% “Some [a single course in neuroanatomy]”; 20% “A little [some exposure in coursework]”; 4% “None”).

Importantly, only 2% of the respondents endorsed the idea that the Classic Model (in a generic sense, not referring to any particular iteration of the model) is the best available theory of language neurobiology. But it is notable that while 90% of respondents endorsed the notion that the Classic Model is outdated, they were split on whether there is a good replacement for the model. Only 24% endorsed the idea that the model should be replaced by another available model from the literature, but 19% suggested that there is not a good replacement. A large number of the respondents (47%) suggested that, while they thought the Classic Model was outdated, they considered that it still served a heuristic function. Thus, the survey reflects a significant range of opinions about the Classic Model. Some support its use. For example, one respondent wrote “The classical model is conceptually correct in many (perhaps...most) ways. Certain details are wrong...[but] the classical model is still a wonderful teaching tool.” In contrast, another respondent wrote “The ‘classic’ model is not a model of language neurobiology. It simply associates poorly defined functions to poorly defined anatomical regions. It

doesn't try to explain how any language-related processes actually happen in the brain.” Several researchers over the last decade have already endorsed the spirit of the latter opinion (see for e.g. [Guenther, 1994, 2006](#); [Hickok & Poeppel, 2004](#); [Poeppel et al., 2012](#)). Yet a literature search conducted in Pubmed and PsycINFO shows that researchers still regularly use the model’s terminology to frame their research questions. Table 1 shows that the use of the terms “Broca” and “Wernicke” is still commonplace in the field.

Insert Table 1 About Here

2. **The Classic Model: History, architecture and functions**

“I like to know where I am. Even if I don’t know where I am, I like to know that.”

-Tom Stoppard, *Rosencrantz and Guildenstern are Dead*, p. 74

The Classic Model, often referred to as the “Broca–Wernicke–Lichtheim- Geschwind model” (e.g. [Geranmayeh et al., 2014](#); [Poeppel & Hickok, 2004](#)), the “Wernicke–Lichtheim–Geschwind model” ([Hagoort, 2013, 2014, 2016](#); [Schwartz, 1984](#)), or simply the “Wernicke-Lichtheim model” ([e.g. Graves, 1997](#)), originates from the pioneer work of researchers in the late 19th century. It should be stated at the outset that the Classic Model is really a family of models—there are important differences in each of the historical instantiations of the Model, and some seem better supported by contemporary evidence than others ([Weiller et al., 2011](#)). However, the Classic Model as most people present and understand it is the revived and reinterpreted version proposed by the neurologist Norman Geschwind ([Geschwind, 1970](#); [Geschwind, 1965a, 1965b](#)). It is essentially Geshwind’s version that is depicted in introductory neuropsychology and medical textbooks, webpages and blogs, despite the fact that it obscures several important aspects of the original theories *en vogue* at the end of the 19th century ([Weiller et al., 2011](#)). This “Geschwind flavored” Classic Model is composed of an anterior inferior frontal area (referred to as “Broca’s area”) and a posterior temporal area (referred to as “Wernicke’s area”). In Geschwind’s version, these regions are connected through a single white-matter pathway, the

arcuate fasciculus, in contrast to the work of Wernicke who explicitly mentioned a second pathway in his later writings ([Wernicke, 1908](#)).

The foundation of the Classic Model can be found in the pioneer clinical work of the French surgeon Paul Broca, who in 1861 first described the posterior two thirds of the inferior frontal gyrus (IFG) as the seat of the ability to articulate language based on observations of brain lesions and associated behavioral consequences. However, Broca did not propose a model of language function. Instead it was the German neurologist Carl Wernicke who, in 1874, described two patients who had difficulty understanding spoken language, even though their articulation was fluent ([Wernicke, 1874/1977](#)). An autopsy conducted by Wernicke on these patients revealed lesions in the superior temporal gyrus, which led Wernicke to conclude that this region was crucial to language comprehension. In the same publication, Wernicke provided one of the first descriptions of a language model based on brain anatomy: “[...] around the Sylvian fissure (S) extends the first primitive convolution. Within this convolution, a₁ is the central end of the acoustic nerve, a its site of entry into the medulla oblongata; b designates the representation of movements governing sound production, and is connected with the preceding through the association fibers a₁b running in the cortex of the insula. From b the efferent pathways of the sound-producing motor nerves run to the oblongata and exit there for the most part [...]” ([Wernicke, 1874, 1874/1977](#)). Wernicke’s model was later clarified and illustrated by Lichtheim ([Lichtheim, 1885](#)). The “Wernicke-Lichtheim model” was revolutionary in its approach to brain-behavior relationships, as it argued for functional specialization of brain regions (which was at the time a controversial topic) and it included as part of the model proposed neuroanatomical pathways that might support communication among the brain regions. The model was extremely useful for organizing the early explorations in language neurobiology as well as for understanding clinical syndromes, in particular the different types of aphasia and agnosia. The model was further elaborated by Lissauer ([Lissauer, 1890](#)), and remained a core neuropsychological model for the following century.

However, applied to contemporary research questions, with current knowledge of brain structure and function, the Classic Model instantiations offer a spatial accuracy that is too limited to test modern hypothesis about brain/behavior relationships. For example, in Figure 1 it is unclear if “*a*” is located within the primary (core) auditory area (i.e., the transverse temporal gyrus, which is the main output of the ascending auditory projections from the medial geniculate body of the thalamus), or in the surrounding secondary (belt) auditory areas. Moreover, “*b*” is not precisely localized within the inferior frontal area, and is assumed to be directly connected to the motor nerves (which we now know to be false).

In addition to a limited spatial precision, another problem with the Classic model is the notion that it has been interpreted as focusing on two interconnected “language epicenters” ([Papathanassiou et al., 2000](#)), “Broca’s and “Wernicke’s areas”, which implies a high degree of functional modularity. This notion was not endorsed by everyone in the early development of the language neurobiology models. For example, writing about his language model, Lichtheim ([1885](#)) stated “I do not consider the function to be localized in one spot of the brain, but rather to result from the combined action of the whole sensorial sphere” (p. 477). Wernicke is in agreement here. For him “only the most elementary psychic functions can be assigned to defined areas of the cortex” and “everything which goes beyond these simplest functions, the association of different impressions into a concept, thinking, consciousness, is an achievement of the fiber tracts which connect the different regions of the cortex to each other”. Thus, Wernicke does appeal to the notion of “language epicenters”, but in his conception language emerges out of their interactions ([Weiller et al., 2011](#)). Despite this, the notion of language centers is central to the Classic Model as it is commonly presented ([Hagoort, 2016](#)). While the importance of inferior frontal and posterior temporal regions for expressive and receptive language functions is not disputed here, evidence that the network supporting language functions is vastly distributed across the brain is now overwhelming. Indeed, speech and language functions engage a very large number of brain regions that extend far beyond “Broca’s and “Wernicke’s areas”, in the frontal, parietal, occipital

and temporal lobes, in the medial hemispheres of the brain, as well as in the basal ganglia, thalamus and cerebellum (for reviews, see for example [Crosson, 2013](#); [Hebb & Ojemann, 2013](#); [Marien et al., 2014](#); [Price, 2010](#)). Hence, despite a tendency in some early writings towards an encompassing rather than a strictly modular approach, language neurobiology framed within the Classic Model has focused almost exclusively on understanding the functions of “Broca’s area” and “Wernicke’s area”.

Hence, the Classic model suffers from at least four major issues: (1) the spatial precision of the model is too limited to test specific hypothesis about brain/behavior relationships; (2) it is centered on two “language regions”, (3) it focuses on cortical structures, and for the most part leaves out subcortical structure and relevant connections¹, and (4) because of its limited spatial extent and cortical focus, it is difficult to reconcile the model with modern knowledge about the white matter connectivity supporting speech and language function.

Despite consensus among many language scientists that the Classic model is outdated ([Poeppe et al., 2012](#)), the model survives, both in terms of the terminology it uses (“Wernicke’s and Broca’s areas”), and in its prevalence. While the model was, and remains, an extremely important milestone in the history of neurosciences, it is often the dominant model presented in undergraduate, graduate, and medical school presentations. In these cases, it is not treated as a historic model, but rather as a model on equal footing with contemporary models of language neurobiology. Furthermore, presentations of this historic model, or variations of it, are often not followed by a presentation of more modern accounts of language neurobiology, leaving the pupil with an inaccurate understanding of modern knowledge about brain and language relationships.

Different versions of the Classic Model are also routinely used in the evaluation and treatment of acquired language disorders, where they fail to account for symptoms resulting from damage to regions or tracts not included in the model, such as the cerebellum and the thalamus. Moreover, because

¹ It should be noted, however, that Wernicke alluded to subcortical structures including the claustrum and cerebellum, in his writings.

moderns accounts on language neurobiology use a variable terminology, sometimes linked to the Model but often not, this makes the integration of research into clinical practice difficult. Arguably clinical practice in speech-language pathology would be facilitated if we all used the same terms to refer to the same brain regions and connections.

3. **There is no consistent definition of Broca's and Wernicke's Areas, and the terms should no longer be used**

"Words, words. They're all we have to go on."

"Consistency is all I ask!"

-Tom Stoppard, *Rosencrantz and Guildenstern are Dead*, pp. 32; 35

Many contemporary researchers continue to state their aims in terms of localizing language function to "Broca's" and "Wernicke's areas" (e.g. [Ardila et al., 2016](#); [Binder, 2015](#); [DeWitt & Rauschecker, 2013](#); [Grodzinsky & Santi, 2008](#); [Hagoort, 2014](#); [Hagoort & van Berkum, 2007](#); [Heim et al., 2002](#); [Kunert et al., 2015](#); [Matchin & Hickok, 2016](#); [Mesulam et al., 2015](#); [Meyer et al., 2012](#); [Santi et al., 2015](#); [Schnur et al., 2009](#); [Thothathiri et al., 2012](#); [Wang et al., 2015](#); [Wise et al., 1999](#)). Yet the field still lacks consistent definition of either region, over 150 years after their initial introduction. This is in keeping with the field of cognitive neuroscience more broadly, which can be ambivalent about anatomical specificity, sometimes advocating precise anatomy, but at other times adopting anatomically ambiguous terminology like "temporo-parietal junction", "inferior frontal junction", and "dorsolateral prefrontal cortex", labeling sulcal locations as the nearest gyrus ([Lancaster et al., 2000](#)), or preferring functional labels without specifying underlying anatomy such as the "visual word form area" or the "premotor cortex". This encourages researchers in the field to conflate functional definitions with anatomical definitions. This approach is, in the long-term, unsustainable if microsurgical, electrostimulation, or genetic interventions for nervous system diseases are to become a reality. Even contemporary neurosurgical interventions that might affect eloquent cortex require precise

targets and a precise neurobiological model of language ([Fujii et al., 2016](#)). An approach focusing on precise anatomy is, of course, not without its own shortcomings—the highly varied structural patterns of the cortical surface across individuals are well-established. However, anatomists have shown that reliable identification is possible despite the variability ([Ono et al., 1990](#); [Tomaiuolo et al., 1999](#)). Moreover, as we hope to show, the definitional problems surrounding Broca’s and Wernicke’s areas are significant, and the continued use of these terms is counterproductive.

The definitional problem is most acute for Wernicke’s area. There has never been a consistent anatomical definition for Wernicke’s area. Indeed, this was a topic of discussion during Professor Mesulam’s keynote address to the Society for the Neurobiology of Language, 2015, in Chicago. Forty years prior, this same problem prompted Bogen and Bogen ([1976](#)) to ask “Wernicke’s region—Where is it?”. No consensus was reached then, and none has been reached since. The confusion can be traced to the very beginning, when Wernicke ([Wernicke, 1874/1977](#)) placed a small dot on the superior temporal gyrus (see Figure 1). The text is clear that Wernicke did not intend the small focused area to represent the “speech center”, and in 1881, he is more specific, drawing a hatched area covering much of the left superior temporal gyrus ([Wernicke, 1881](#)). Despite this, almost immediately, the definition undergoes significant revision by Wernicke’s contemporaries. In some cases, the region is simply on and around the superior temporal gyrus. In other cases, it extends widely to include the inferior parietal lobe, and middle temporal gyrus.

This lack of specificity is, at least partly, attributable to the fact that patients presenting with a “posterior lesion” and presenting with language comprehension deficits were historically referred to as “Wernicke’s aphasics”, even when the lesion was incongruent with Wernicke’s writings. This issue can be alleviated by using a symptom-based classification of the aphasias rather than a lesion-based approach (for instance, referring to fluent rather than Wernicke’s aphasia), an approach that is gaining support in speech-language pathology. Lesions can be described in more precise anatomical terms, such as “posterior third of the superior temporal gyrus” or “anterior third of the supramarginal gyrus”.

But the fact remains that, throughout the twentieth century, almost every patch of perisylvian temporal and inferior parietal cortex has been presented to fall under the definition of Wernicke's area ([Bogen & Bogen, 1976](#)).

Our survey suggests that, despite various historical attempts to define the area, there is still no consensus. Respondents seemed to prefer two anatomical definitions of "Wernicke's area", but neither garnered more than 30% of the votes. The most popular anatomical definition is one that we provided ourselves (marked "Authors' definition" in Figure 2, covering the posterior part of the superior temporal gyrus and including part of the supramarginal gyrus), and which is not found in any published paper (to our knowledge), nor based on any empirical study (although it, like Lewandowsky's definition, closely resembles Geschwind's 1972 definition).

The second most popular anatomical definition of "Wernicke's area" is based on Geschwind ([1970](#)); marked "Geschwind, 1970" in Figure 2, covering only the posterior part of the superior temporal gyrus), and is also the most recent published definition we included. 12% of respondents did not provide a vote, and instead provided various comments such as "the term is meaningless", or "it seems that these are all possibilities, depending on what you read". Definitions that included the posterior middle temporal gyrus and inferior parietal lobule were unpopular, despite evidence for the importance of these regions in language comprehension ([Dronkers et al., 2004](#); [Mesulam et al., 2015](#)). Only 8% of respondents favored Wernicke's (1881) original definition. Thus, even among experts within the field of language neurobiology, there is still no consensus definition of Wernicke's area.

Broca's area is a smaller piece of cortex than Wernicke's area, and so might be expected that a consensus could be reached. Indeed, Bogen and Bogen ([Bogen & Bogen, 1976](#)) suggest that there has always been agreement about the location of Broca's area in the posterior *third* of the IFG. Wernicke is equally confident: "As is well-known, [Broca] localized the faculty of speech to the posterior portion of the so-called third frontal gyrus...That is that portion of the most inferior and external part of the operculum, located in the frontal part of the central gyrus, just anterior to its juncture."([Wernicke,](#)

[1874/1977, pp. 70-71](#)). But this is not the case—from the earliest definition, there was debate ([Lorch, 2008](#)). The report of the meeting of the Norwich British Association for the Advancement of Science shows that while Broca proposed that the region for articulated language was confined to the posterior part of the IFG (*The Lancet*, 92, 1868: 293, reported in Lorch ([2008](#))), other meeting attendees suggested that the evidence, presented as diagrams and plaster casts, showed a larger extent ([Dickson, 1868](#)). A re-evaluation using magnetic resonance imaging (MRI) of the original brain of Broca’s patient Leborgne suggests that the lesion indeed included the posterior part of the IFG but also extended beyond it ([Dronkers et al., 2007](#)).

However, the field has not restricted the definition to that defined on Leborgne. For example, a popular definition is that Broca’s area is synonymous with the left IFG, which Mesulam (2015; p. 2424) argues is a designation so widely accepted “that its location is no longer a subject of scientific debate.” Yet, on the contrary, our survey of language researchers suggests that a lack of consensus remains. Only 23% of survey respondents agreed with Mesulam’s definition ([Mesulam et al., 2015](#)), and only 8% agreed with Bogen and Bogen ([1976](#)); this is also Dejerine’s (1914) definition). A larger percentage (50%) chose the region comprised of the *pars triangularis* and *pars opercularis*, which, though a high percentage, still reflects the lack of a strong consensus (it does not reach a simple majority).

The survey suggests that search for a consistent anatomical definition for “Broca’s and Wernicke’s areas” is a Sisyphean task. First and foremost, anatomically, the regions typically referred to as Broca’s and Wernicke’s areas are large enough such that they do not have cytoarchitectonic and myeloarchitectonic homogeneity. Although this has been known since the early twentieth century ([Brodmann, 2006](#); [Campbell, 1905](#); [Smith, 1907](#); [Vogt & Vogt, 1919](#); [Von Economo & Koskinas, 1925](#)) and has been shown repeatedly in recent years ([Amunts et al., 2010](#); [Amunts & Zilles, 2012](#); [Annese et al., 2004](#); [Goucha & Friederici, 2015](#); [Zilles & Amunts, 2012](#); [Zilles et al., 1997](#)), the initial definitions of Broca’s and Wernicke’s areas precede the major findings in this area of investigation.

This is even the case for Broca's area, which by most definitions is a relatively circumscribed patch of cortex ([Petrides et al., 2005](#)). Anatomical heterogeneity is naturally coupled with functional heterogeneity. For example, a number of studies have suggested a dissociation between semantic and phonological processing within anterior and posterior regions of the IFG (e.g., [Katzev et al., 2013](#); [Price, 2010](#)). Because the specific functions or sets of functions with which each patch of cortex is involved are still under investigation, it is even more important to be careful and precise about which parts of the brain we are referring. Binder ([2015](#)) recently argued for a similar conclusion for Wernicke's area, noting that "speech comprehension is a highly distributed function, involving a bi-hemispheric phoneme perception system and a widely distributed semantic network. To refer to all of these regions as the Wernicke area seems to sacrifice any utility that the term might have..." (p. 5). However, instead of rejecting the label, he suggests that we retain the Wernicke label and re-define the function of the region. Rather than continue to search for the functions of Broca's and Wernicke's areas, we argue for the opposite, namely that we should simply retire the labels.

Why should the labels be retired? The reason is that the vocabulary in use in any scientific endeavor matters, and continued conceptual work and elaboration and revision of the standard vocabulary of the field is a necessary feature of science. We can and do become "captives of a ... set of verbal categories" (Searle, 1992; p. 31). We inherit this vocabulary from the giants of previous generations and "with the vocabulary a certain set of categories, within which we are historically conditioned to think about [the] problems. The vocabulary is not innocent, because implicit in the vocabulary are a surprising number of theoretical claims" ([Searle, 1992, p. 14](#)). Paradigmatic changes, which are occurring in the field of language neurobiology, cause scientists to see the world of their research engagement differently, and these changes cause "old terms, concepts and experiments fall into new relationships one with the other" ([Kuhn, 1970, p. 149](#)). The terms Broca's and Wernicke's Areas are not innocuous terms—they carry with them a notion of functional relevance to language, but not everyone agrees on their anatomical definition, and not everyone agrees on their function. This

contributes to significant conceptual confusion, and, outside of a historical review context, there is simply no reason to continue to use them for contemporary theories.

To illustrate the issue with respect to Broca's area, we encourage the reader to examine Hagoort's recent Memory, Unification, and Control model ([Hagoort, 2016](#)). It is notable that Hagoort begins this examination with a brief review of the Classic Model, states that it is a historical model, and then initially continues to work within that framework, using the terminology of Broca's and Wernicke's areas. For example, in the first figure of the paper (Figure 28.1), the function of "Unification requires the contribution of Broca's area (Brodmann areas 44 and 45) and adjacent cortex (Brodmann areas 47 and 6) in the frontal lobe" (p. 340). It is difficult, though, for Hagoort to work within this framework for long, because if he does so, he does not go very far toward advancing a new theory that is different in major respects from the Classic Model. His pivot is to take seriously the notion that "language is subserved by dynamic networks of brain regions." (p. 340). With this perspective in hand, Hagoort is careful to break up Broca's and Wernicke's regions into smaller anatomical parts, as we advocate. For example, his model parses the sub-regions of the IFG into *pars opercularis*, *pars triangularis*, and *pars orbitalis*, which he notes have different associated connectivity and functions. He does the same with the temporal and parietal lobes—in this way his model evolves to having nine nodes supporting language function, anchored by a network of fiber pathways (which we review in the next section). Thus, in order to present his new model, he makes a significant break with the Classic Model, even closing his exposition with a section titled "Beyond the Classical Model". Hagoort shows that the Classic Model terminology is too constraining, for him, to develop a serious model of language neurobiology in the face of new thinking about network architectures supporting cognition, which requires the specification of multiple interacting nodes within the network, and serious reflection on their connectivity. The new model specification is also more amenable to empirical assessment using more modern analytic techniques, such as network analysis ([Sporns, 2011](#)). The Classic Model cannot be tested with such techniques because, as a two-node, one connection model, it is too simple.

To illustrate the definitional issue with respect to Wernicke's area, we point to DeWitt and Rauschecker's recent paper ([DeWitt & Rauschecker, 2013](#)). A central focus of their paper is to re-locate Wernicke's area. Thus, they write:

“Where is Wernicke's area? Answering this question today—with the benefit of far greater understanding of neuroanatomy and cortical processing than either Wernicke or Geschwind had access to—we might conclude that the functions Wernicke subsumes within a single area are actually performed by multiple cortical areas... The hypothesis most strongly supported by available empirical data for the location of Wernicke's AWFA [auditory word form area] is anterior STG [superior temporal gyrus]... This region, however, is neither a strong candidate site for encoding representations that resemble Wernicke's word-concepts (*i.e.*, inner speech) nor for performing the corrective function Wernicke ascribes to them.” (p. 186).

But the question we are trying to address as a field is not “Where is Wernicke's area?” A more interesting question, we believe, might be: How does the brain accomplish and integrate the various sub-functions that comprise human language, can we parse the network implementing these sub-functions into its constituent components, and can we identify the role specific patches of cortex (or subcortical nuclei or regions) play in the context of the broader system implementing language? For DeWitt and Rauschecker, the question is more specifically “where are the patches of cortex associated with auditory word form recognition?” But instead of addressing this question, DeWitt and Rauschecker (2013) continue to try to localize Wernicke's area. At the end of their investigation they write: “Wernicke's area, functionally defined, therefore appears to consist of two areas: an AWFA in anterior STG and an “inner-speech area” in posterior [superior temporal gyrus/inferior parietal lobule] STG/IPL” (p. 187). It would be more productive, in our opinion, to simply try to define the network for auditory word recognition, rather than come up with yet another definition of Wernicke's area.

Hagoort and DeWitt and Rauschecker show us that the use of the terms “Broca’s and Wernicke’s areas” are still in wide use, still frame a lot of the models and model-building steps in language neurobiology, and carry historical conceptual baggage that slows theoretical advance. In the place of the use of the Broca and Wernicke terminology, we suggest following the lead advocated by others before us ([Devlin & Poldrack, 2007](#); [Toga & Thompson, 2007](#))—anatomical definitions with reference to a published atlas are preferred over poorly defined functional labels. Our thesis is also an endorsement of precise neuroanatomy for any model of language neurobiology. Brodmann, over a hundred years ago, wrote: “*functional localization of the cerebral cortex without the lead of anatomy is utterly impossible...In all domains, physiology has its firmest foundations in anatomy.*” ([Brodmann, 1909](#); [2006, p. 262](#)). Wernicke was himself a precise anatomist in the school of Meynert ([Gage & Hickok, 2005](#)), and the field could benefit by emulating that precision.

Obviously, the Classic Model developed in the 19th and 20th centuries is not based on modern macroscopical neuroanatomy. Because our knowledge of brain anatomy and function has evolved, it seems more productive to build new models based modern terminologies and clear anatomical definitions. Thus we advocate a clean break from the Classic Model and its associated terminology. Reliable anatomical definitions and reporting of findings in more specific anatomical landmarks will also facilitate the definition of the broader language network, including its connectivity. Understanding of this “language connectome”—the white matter connectivity of the perisylvian regions associated with speech and language—has expanded rapidly in the last decade, and further supports our argument that the classic model is not sustainable as a useful model of language neurobiology. The recent evolution of this literature is briefly summarized in the next section.

4. Fiber pathways supporting speech and language: beyond the arcuate fasciculus

“What a fine persecution—to be kept intrigued without ever quite being enlightened.”

-Tom Stoppard, *Rosencrantz and Guildenstern are Dead*, p. 32

The fiber pathway connectivity that support speech and language functions has come under intense scrutiny in the last decade, largely due to the advent of advanced diffusion-weighted imaging techniques that can map fiber pathways *in vivo*, even though, as Saur (2015) concisely states, “precise long-distant region-to-region structural connectivity between lobes is still difficult to obtain and represents one of the greatest challenges in systems neuroscience.” In short, a comprehensive mapping of the “language connectome” remains elusive. It is within this context that we consider the role of the arcuate fasciculus (AF) as the “language pathway” of the Classic model.

In blunt fiber dissection, the core fibers of the AF (historically also the superior longitudinal fasciculus; SLF) are easily identifiable, and definition of the pathway appeared in Burdach’s early anatomical treatments of the 19th century (Burdach, 1819-1826). In his original treatise Wernicke (Wernicke, 1874/1969) refers to this pathway as “association fibers”, the “path a₁b” or “fibra propria”, which connects inferior frontal and temporal regions to support speech and language. There are also a few mentions of a “fibrae arcuatae” throughout the article. It is von Monakow (1897), though, who more explicitly names these fibers, and the AF is established as the “language pathway” over the 20th century, notably by Geschwind (1970); Wernicke later agreed that the arcuate fasciculus was a language pathway; Wernicke, 1908).

Contemporary research suggests that the notion that a single fiber pathway supports language function in the human brain should be considered obsolete (even the two pathways, uncinata fasciculus and arcuate fasciculus, that Wernicke (Wernicke, 1908) advocated are insufficient (see Weiller et al., 2011 for an account of the history of the “lost” ventral tract). Modern perspectives on language connectivity should consider several sets of association pathways: fronto-temporal, parieto-temporal, occipito-temporal, and fronto-frontal connections (see Figure 4), as well as thalamic radiations, and

cortico-subcortical loops connecting the cortex to the basal ganglia, cerebellum, midbrain and pontine nuclei. A brief review of the different pathways that may support language functions is presented below (and more comprehensively elsewhere; see [Axer et al., 2013](#); [Dick et al., 2014](#); [Dick & Tremblay, 2012](#); [Gierhan, 2013](#); [Saur et al., 2008](#); [Weiller et al., 2011](#)).

Fronto-temporal connections supporting language functions include, in addition to the AF, the uncinate fasciculus (UF), extreme capsule/extreme capsule fiber system (EmC), and the inferior fronto-occipital fasciculus (IFOF). The UF connects the orbital and lateral frontal cortex with the temporal pole, anterior temporal cortex, parahippocampal gyrus, and amygdala ([Von Der Heide et al., 2013](#)). Some investigators believe the UF to be associated with semantic processing, given its strong connectivity with the anterior temporal cortex and temporal pole, a proposed “hub” for semantic processing ([Holland & Lambon Ralph, 2010](#)). Evidence for loss of semantic function (e.g., picture naming deficits) following resection of the UF supports this notion ([Papagno et al., 2011](#)), but this is not without controversy ([Kho et al., 2008](#); [Moritz-Gasser et al., 2013](#)). Another fronto-temporal connection, the EmC or “extreme capsule fiber system” is a collection of axons located between the claustrum (medially) and the insula (laterally). Some evidence in the human suggests that EmC connects the ventral and lateral frontal lobe with the most of the superior and middle temporal cortex, extending anterior-to-posterior ([Makris & Pandya, 2009](#); [Saur et al., 2008](#)). Such a pathway could provide an alternative route between the anterior inferior frontal and temporal lobes, which may support syntactic and semantic processing ([Griffiths et al., 2013](#); [Rolheiser et al., 2011](#)). Finally, the IFOF originates in the inferior and medial occipital lobe (and possibly the medial parietal lobe), sends projections to the ventral temporal lobe, and travels through the temporal stem to project to the IFG, the medial and orbital frontal cortex, and the frontal pole ([Catani et al., 2003](#); [Sarubbo et al., 2013](#)). Duffau and colleagues ([Martino et al., 2013](#)) have suggested that the IFOF is a “direct” pathway anchoring the ventral semantic system for language, but additional research is needed to understand whether these different pathways operate as part of non-language networks, which may offer alternative

interpretations of their functions.

Parieto-temporal and occipito-temporal connections include the middle longitudinal fasciculus (MdLF) and inferior longitudinal fasciculus (ILF). The MdLF is well-established in the macaque ([Schmahmann & Pandya, 2006](#); [Seltzer & Pandya, 1994](#)), but less so in the human ([Makris & Pandya, 2009](#); [Makris et al., 2013a](#); [Makris et al., 2013b](#); [Maldonado et al., 2013](#); [Saur et al., 2008](#); [Turken & Dronkers, 2011](#); [Wang et al., 2013](#)). The available evidence suggests that the MdLF originates in the posterior superior temporal, inferior and superior parietal lobe, and possibly occipital lobe, producing terminations along the course of the temporal cortex to the temporal pole. It may thus be important for language comprehension ([Turken & Dronkers, 2011](#)) or semantic processing ([Saur et al., 2008](#)), although some question its role in language ([Wang et al., 2013](#)). The ILF connects the occipital lobe with the temporal lobe, originating in secondary visual areas and connecting to the middle and inferior temporal gyri, the temporal pole, parahippocampal gyrus, hippocampus, and amygdala ([Catani et al., 2003](#)). Several authors have suggested that the ILF is a major component of a ventral system supporting semantic processes ([Agosta et al., 2013](#); [Saur et al., 2008](#); [Turken & Dronkers, 2011](#)). If we expand the focus to paralinguistic functions such as literacy, a recently re-discovered fiber pathway ([Yeatman et al., 2014](#)), the vertical occipital fasciculus (VOF), becomes yet another potentially important pathway². This pathway appears to connect the lateral occipitotemporal sulcus and gyrus (associated with the processing of visual word forms) with inferior, and possibly superior, parietal regions that are important for literacy and numeracy ([Bouhali et al., 2014](#); [Greenblatt, 1973, 1976](#); [Yeatman et al., 2013](#)).

To date, much of the research on perisylvian long association fiber pathways has focused on speech perception and language comprehension, and has largely neglected the contribution of cortical and subcortical networks for speech production. But speech production was, of course, a major

² It was, incidentally, Wernicke who first named and defined this pathway, which he called the perpendicular occipital fasciculus, in his 1881-1883 *Lehrbuch der Gehirnkrankheiten für Aerzte und Studierende*. 3 Volumes. Kassel: Fischer.

component of the Classic Model from the earliest description of Broca's patient Leborgne and other case-studies with Broca's aphasia. Additional fiber pathways of the cortico-bulbar, cortico-cerebellar, and cortico-striatal systems are known to support speech production. Even fronto-frontal fiber pathways only recently identified in children and adults using diffusion-weighted MRI, such as the frontal aslant tract (FAT; [Broce et al., 2015](#); [Catani et al., 2013](#)) (Figure 5), which connects the inferior frontal regions with the pre-supplementary motor area, may play a role in spoken language production ([see Dick et al., 2014 for a more detailed review](#)).

The Classic Model as it is most commonly presented in contemporary textbooks, with a single connection between two central nodes, is thus insufficient to account for the overwhelming evidence that multiple fiber pathways support language function in the human brain. Since all these pathways may make important contributions to a variety of linguistic functions, there is no reason to continue to focus on a single pathway. Moreover, returning to the issue of language-centricity, it will be important to examine the contributions of each of the pathways to other cognitive and sensorimotor functions in order to better understand the computations that they may be involved with during the processing and production of language.

5. Conclusions, or where to go from here.

"...look on every exit being an entrance somewhere else."

-Tom Stoppard, *Rosencrantz and Guildenstern are Dead*, p. 21

The central thesis of this article is that the Classic Model, in its most common iteration, is neither an anatomically precise nor a comprehensive model of language neurobiology ([cf. Poeppel, 2014](#)), and that the maintenance of the terminology of this model artificially maintains it as a legitimate model. Although the field as a whole has made tremendous progress in the past few decades, due in part to significant advances in the neuroimaging and neurostimulation methods, we believe abandoning

the Classic Model and the terminology of Broca's and Wernicke's areas would provide a catalyst for additional theoretical advancement.

Focusing on the Classic Model has, we believe, limited our attention to a rich theoretical and empirical literature that tries to bring to the forefront important notions about the neurobiology of language: a distributed architecture which includes cortical and subcortical components, a distributed anatomical connectivity, and, perhaps most importantly, a heavy reliance on domain-general neural resources (e.g. [Bornkessel-Schlesewsky et al., 2015](#); [Rijntjes et al., 2012](#)). Understanding how language functions are organised in the brain and how they relate to other functions is, no doubt, a critical issue: *“The most fundamental question in the study of the human language faculty is its place in the natural world: what kind of biological system it is, and how it relates to other systems in our own species and others”* ([Pinker & Jackendoff, 2005](#)). Because the simple architecture of the Classic Model suggests a language-centric perspective, the resilience of the model has perpetuated different flavors of the longstanding idea that the neural machinery for language is “special”, that is, the notion that there exists neural tissue dedicated to the specific task of processing and producing language. An alternative view is that language is, at least in part, an overlaid functional system that *“gets what service it can out of nervous tissues that have come into being and are maintained for very different ends than its own”* ([adapted from Sapir, 1921](#)). Although some language-specific mechanisms may exist, our emerging understanding of brain function is of mutual interactions and common control mechanisms. Wernicke, over 140 years ago, was already on the right track—*“a priori reasoning would view restriction of the speech center to a single area, namely, Broca's gyrus, as highly improbable”* (Wernicke, 1874/1994; p. 74). As a field, we need to study the interactions between language and other functional systems in order to fully understand the neurobiological underpinning of human language and language disorders, and the degree to which it is dependent upon various other cognitive, sensorimotor and emotional processes, all of which must come together to put language into action. Consistent with these notions, most contemporary models of the neurobiology of language propose a much more complex architecture

encompassing regions that had never before been considered to support language functions. Though we agree with those who have completed our survey that there is not one clear, comprehensive alternative, we do think there are a number of promising developments ([Ballard et al., 2003](#); [Binder & Desai, 2011](#); [Binder et al., 2009](#); [Bornkessel-Schlesewsky et al., 2015](#); [Duffau et al., 2014](#); [Friederici & Singer, 2015](#); [Guenther, 2006](#); [Hagoort, 2013, 2014, 2016](#); [Hickok, 2009, 2014](#); [Hickok et al., 2002](#); [Hickok & Poeppel, 2004, 2007](#); [Hickok & Poeppel, 2000](#); [Mesulam et al., 2015](#); [Price, 2010](#); [Rauschecker & Scott, 2009](#); [Scott & Johnsrude, 2003](#); [Skeide & Friederici, 2016](#)), each presenting a more comprehensive architecture for language than the Classic Model. In fact, to many researchers we may be “preaching to the choir”. However, our analysis of the literature clearly reveals that the Classic Model, or at the very least its terminology, is still robust. We would urge the field of language neurobiology as a whole to consider these other promising avenues on which to establish a new, comprehensive alternative to the Classic Model.

6. **Acknowledgments**

P. Tremblay holds a Career Award from the “Fonds de Recherche du Québec – Santé” (FRQS).

We thank Michael Andric and Uri Hasson for their comments on previous versions of this manuscript.

We also thank everyone who answered our online Survey.

7. **References**

- Agosta, F., Galantucci, S., Canu, E., Cappa, S. F., Magnani, G., Franceschi, M., . . . Filippi, M. (2013). Disruption of structural connectivity along the dorsal and ventral language pathways in patients with nonfluent and semantic variant primary progressive aphasia: a DT MRI study and a literature review. *Brain Lang*, *127*(2), 157-166. doi: 10.1016/j.bandl.2013.06.003
- Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., & Zilles, K. (2010). Broca's region: novel organizational principles and multiple receptor mapping. *PLoS Biology*, *8*(9). doi: 10.1371/journal.pbio.1000489
- Amunts, K., & Zilles, K. (2012). Architecture and organizational principles of Broca's region. *Trends Cogn Sci*, *16*(8), 418-426. doi: 10.1016/j.tics.2012.06.005
- Annese, J., Pitiot, A., Dinov, I. D., & Toga, A. W. (2004). A myelo-architectonic method for the structural classification of cortical areas. *Neuroimage*, *21*(1), 15-26.

- Ardila, A., Bernal, B., & Rosselli, M. (2016). [The language area of the brain: a functional reassessment]. *Rev Neurol*, 62(3), 97-106.
- Axer, H., Klingner, C. M., & Prescher, A. (2013). Fiber anatomy of dorsal and ventral language streams. *Brain Lang*, 127(2), 192-204. doi: 10.1016/j.bandl.2012.04.015
- Ballard, K.J., Robin, D.A., & Folkins, J.W. (2003). An integrative model of speech motor control: A response to Ziegler. *Aphasiology*, 17(1), 37-48.
- Binder, J. R. (2015). The Wernicke area: Modern evidence and a reinterpretation. *Neurology*. doi: 10.1212/WNL.0000000000002219
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends Cogn Sci*, 15(11), 527-536. doi: 10.1016/j.tics.2011.10.001
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, 19(12), 2767-2796. doi: 10.1093/cercor/bhp055
- Bogen, J. E., & Bogen, G. M. (1976). Wernicke's region--Where is it? *Ann N Y Acad Sci*, 280, 834-843.
- Bornkessel-Schlesewsky, I., Schlewsky, M., Small, S. L., & Rauschecker, J. P. (2015). Neurobiological roots of language in primate audition: common computational properties. *Trends Cogn Sci*, 19(3), 142-150. doi: 10.1016/j.tics.2014.12.008
- Bouhali, F., Thiebaut de Schotten, M., Pinel, P., Poupon, C., Mangin, J. F., Dehaene, S., & Cohen, L. (2014). Anatomical connections of the visual word form area. *J Neurosci*, 34(46), 15402-15414. doi: 10.1523/JNEUROSCI.4918-13.2014
- Broce, I., Bernal, B., Altman, N., Tremblay, P., & Dick, A. S. (2015). Fiber tracking of the frontal aslant tract and subcomponents of the arcuate fasciculus in 5-8-year-olds: Relation to speech and language function. *Brain Lang*, 149, 66-76. doi: 10.1016/j.bandl.2015.06.006
- Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Gro hirnrinde*. Leipzig: Verlag von Johann Ambrosius Barth.
- Brodmann, K. (2006). *Brodmann's Localisation in the Cerebral Cortex* (L. J. Garey, Trans.): Springer.
- Burdach, K. F. (1819-1826). *Vom bau und leben des gehirns und rückenmarks (3 vols)*. Leipzig: In der dyk'schen buchhandlung.
- Campbell, A.W. (1905). *Histological studies on the localisation of cerebral function*. Cambridge, UK: University Press.
- Catani, M., Jones, D K, & ffytche, D H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology*, 57, 8-16.
- Catani, M., Jones, D. K., Donato, R., & Ffytche, D. H. (2003). Occipito-temporal connections in the human brain. *Brain*, 126(Pt 9), 2093-2107. doi: 10.1093/brain/awg203
- Catani, M., Mesulam, M.M., Jakobsen, E., Malik, F., Martersteck, A., Wieneke, C., . . . Rogalski, E. (2013). A novel frontal pathway underlies verbal fluency in primary progressive aphasia. *Brain*, 136(Pt 8), 2619-2628. doi: 10.1093/brain/awt163
- Crosson, B. (2013). Thalamic mechanisms in language: a reconsideration based on recent findings and concepts. *Brain Lang*, 126(1), 73-88. doi: 10.1016/j.bandl.2012.06.011
- Devlin, J. T., & Poldrack, R. A. (2007). In praise of tedious anatomy. *Neuroimage*, 37(4), 1033-1041; discussion 1050-1038. doi: 10.1016/j.neuroimage.2006.09.055
- DeWitt, I., & Rauschecker, J. P. (2013). Wernicke's area revisited: parallel streams and word processing. *Brain Lang*, 127(2), 181-191.
- Dick, A, Bernal, B., & Tremblay, P. (2014). The language connectome: New pathways, new concepts. *The Neuroscientist*, 20, 453-467.
- Dick, A. S., & Tremblay, P. (2012). Beyond the arcuate fasciculus: consensus and controversy in the connectional anatomy of language. *Brain*, 135(Pt 12), 3529-3550. doi: 10.1093/brain/aws222
- Dickson, J.T. (1868). Reports of Society. *Br Med J*. doi: <http://dx.doi.org/10.1136/bmj.2.401.259>

- Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, *130*(Pt 5), 1432-1441. doi: awm042 [pii]
10.1093/brain/awm042
- Dronkers, Nina F., Wilkins, David P., Van Valin Jr, Robert D., Redfern, Brenda B., & Jaeger, Jeri J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, *92*(1-2), 145-177.
- Duffau, H., Moritz-Gasser, S., & Mandonnet, E. (2014). A re-examination of neural basis of language processing: proposal of a dynamic hodotopical model from data provided by brain stimulation mapping during picture naming. *Brain Lang*, *131*, 1-10. doi: 10.1016/j.bandl.2013.05.011
- Friederici, A. D., & Singer, W. (2015). Grounding language processing on basic neurophysiological principles. *Trends Cogn Sci*, *19*(6), 329-338. doi: 10.1016/j.tics.2015.03.012
- Fujii, M., Maesawa, S., Ishiai, S., Iwami, K., Futamura, M., & Saito, K. (2016). Neural Basis of Language: An Overview of An Evolving Model. *Neurol Med Chir (Tokyo)*. doi: 10.2176/nmc.ra.2016-0014
- Gage, N., & Hickok, G. (2005). Multiregional cell assemblies, temporal binding and the representation of conceptual knowledge in cortex: a modern theory by a "classical" neurologist, Carl Wernicke. *Cortex; a journal devoted to the study of the nervous system and behavior*, *41*(6), 823-832.
- Geranmayeh, F., Brownsett, S. L., & Wise, R. J. (2014). Task-induced brain activity in aphasic stroke patients: what is driving recovery? *Brain*, *137*(Pt 10), 2632-2648. doi: 10.1093/brain/awu163
- Geschwind, N. (1970). The organization of language and the brain. *Science*, *170*, 940-944.
- Geschwind, Norman. (1965a). Disconnexion syndromes in animals and man: Part I. *Brain*, *88*(2), 237-294. doi: 10.1093/brain/88.2.237
- Geschwind, Norman. (1965b). Disconnexion syndromes in animals and man: Part II. *Brain*, *88*(3), 585-644. doi: 10.1093/brain/88.3.585
- Gierhan, S. M. (2013). Connections for auditory language in the human brain. *Brain Lang*, *127*(2), 205-221. doi: 10.1016/j.bandl.2012.11.002
- Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca's Area. *Neuroimage*, *114*, 294-302. doi: 10.1016/j.neuroimage.2015.04.011
- Graves, R. E. (1997). The legacy of the Wernicke-Lichtheim model. *J Hist Neurosci*, *6*(1), 3-20. doi: 10.1080/09647049709525682
- Greenblatt, S. H. (1973). Alexia without agraphia or hemianopsia anatomical analysis of an autopsied case. *Brain : A Journal of Neurology*, *96*(2), 307-316.
- Greenblatt, S. H. (1976). Subangular alexia without agraphia or hemianopsia. *Brain and language*, *3*(2), 229-245.
- Griffiths, J. D., Marslen-Wilson, W. D., Stamatakis, E. A., & Tyler, L. K. (2013). Functional organization of the neural language system: dorsal and ventral pathways are critical for syntax. *Cereb Cortex*, *23*(1), 139-147. doi: 10.1093/cercor/bhr386
- Grodzinsky, Y., & Santi, A. (2008). The battle for Broca's region. *Trends Cogn Sci*, *12*(12), 474-480. doi: 10.1016/j.tics.2008.09.001
- Guenther, F.H. (1994). A neural network model of speech acquisition and motor equivalent speech production. *Biol Cybern*, *72*(1), 43-53.
- Guenther, F.H. (2006). Cortical interactions underlying the production of speech sounds. *J Commun Disord*, *39*(5), 350-365. doi: 10.1016/j.jcomdis.2006.06.013
- Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Front Psychol*, *4*, 416. doi: 10.3389/fpsyg.2013.00416

- Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Curr Opin Neurobiol*, 28, 136-141. doi: 10.1016/j.conb.2014.07.013
- Hagoort, P. (2016). Chapter 28 – MUC (Memory, Unification, Control): A Model on the Neurobiology of Language Beyond Single Word Processing. In G. Hickok & S. L. Small (Eds.), *Neurobiology of language*: Elsevier.
- Hagoort, P., & van Berkum, J. (2007). Beyond the sentence given. *Philos Trans R Soc Lond B Biol Sci*, 362(1481), 801-811. doi: 10.1098/rstb.2007.2089
- Hebb, A. O., & Ojemann, G. A. (2013). The thalamus and language revisited. *Brain Lang*, 126(1), 99-108. doi: 10.1016/j.bandl.2012.06.010
- Heim, S., Opitz, B., & Friederici, A. D. (2002). Broca's area in the human brain is involved in the selection of grammatical gender for language production: evidence from event-related functional magnetic resonance imaging. *Neurosci Lett*, 328(2), 101-104.
- Hickok, G. (2009). The functional neuroanatomy of language. *Phys Life Rev*, 6(3), 121-143. doi: 10.1016/j.pprev.2009.06.001
- Hickok, G. (2014). The architecture of speech production and the role of the phoneme in speech processing. *Lang Cogn Process*, 29(1), 2-20. doi: 10.1080/01690965.2013.834370
- Hickok, G., Love-Geffen, T., & Klima, E. S. (2002). Role of the left hemisphere in sign language comprehension. *Brain Lang*, 82(2), 167-178.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1-2), 67-99. doi: 10.1016/j.cognition.2003.10.011
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393-402.
- Hickok, Gregory, & Poeppel, David. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences*, 4(4), 131-138.
- Holland, R., & Lambon Ralph, M. A. (2010). The anterior temporal lobe semantic hub is a part of the language neural network: selective disruption of irregular past tense verbs by rTMS. *Cereb Cortex*, 20(12), 2771-2775. doi: 10.1093/cercor/bhq020
- Katzev, M., Tuscher, O., Hennig, J., Weiller, C., & Kaller, C. P. (2013). Revisiting the functional specialization of left inferior frontal gyrus in phonological and semantic fluency: the crucial role of task demands and individual ability. *J Neurosci*, 33(18), 7837-7845. doi: 10.1523/JNEUROSCI.3147-12.2013
- Kho, K. H., Indefrey, P., Hagoort, P., van Veelen, C. W., van Rijen, P. C., & Ramsey, N. F. (2008). Unimpaired sentence comprehension after anterior temporal cortex resection. *Neuropsychologia*, 46(4), 1170-1178. doi: 10.1016/j.neuropsychologia.2007.10.014
- Kuhn, T.S. (1970). *The Structure of Scientific Revolutions* Chicago: The University of Chicago Press.
- Kunert, R., Willems, R. M., Casasanto, D., Patel, A. D., & Hagoort, P. (2015). Music and Language Syntax Interact in Broca's Area: An fMRI Study. *PLoS One*, 10(11), e0141069. doi: 10.1371/journal.pone.0141069
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., . . . Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Hum Brain Mapp*, 10(3), 120-131.
- Lichtheim, L. (1885). On aphasia. *Brain*, 433-484.
- Lissauer, H. (1890). Ein Fall von Seelenblindheit nebst einem Beitrag zur Theorie derselben. [A case of visual agnosia with a contribution to theory]. *Archiv für Psychiatrie*, 21, 222-270.
- Lorch, M. P. (2008). The merest Logomachy: The 1868 Norwich discussion of aphasia by Hughlings Jackson and Broca. *Brain*, 131(Pt 6), 1658-1670. doi: 10.1093/brain/awn058
- Makris, N., & Pandya, D. N. (2009). The extreme capsule in humans and rethinking of the language circuitry. *Brain Structure and Function*, 213, 343-358.

- Makris, N., Preti, M. G., Asami, T., Pelavin, P., Campbell, B., Papadimitriou, G. M., . . . Kubicki, M. (2013a). Human middle longitudinal fascicle: variations in patterns of anatomical connections. *Brain Struct Funct*, 218(4), 951-968. doi: 10.1007/s00429-012-0441-2
- Makris, N., Preti, M. G., Wassermann, D., Rathi, Y., Papadimitriou, G. M., Yergatian, C., . . . Kubicki, M. (2013b). Human middle longitudinal fascicle: segregation and behavioral-clinical implications of two distinct fiber connections linking temporal pole and superior temporal gyrus with the angular gyrus or superior parietal lobule using multi-tensor tractography. *Brain Imaging Behav*, 7(3), 335-352. doi: 10.1007/s11682-013-9235-2
- Maldonado, I. L., de Champfleury, N. M., Velut, S., Destrieux, C., Zemmoura, I., & Duffau, H. (2013). Evidence of a middle longitudinal fasciculus in the human brain from fiber dissection. *J Anat*, 223(1), 38-45. doi: 10.1111/joa.12055
- Marien, P., Ackermann, H., Adamaszek, M., Barwood, C. H., Beaton, A., Desmond, J., . . . Ziegler, W. (2014). Consensus paper: Language and the cerebellum: an ongoing enigma. *Cerebellum*, 13(3), 386-410. doi: 10.1007/s12311-013-0540-5
- Martino, Juan, De Witt Hamer, Philip C, Berger, Mitchel S, Lawton, Michael T, Arnold, Christine M, de Lucas, Enrique Marco, & Duffau, Hugues. (2013). Analysis of the subcomponents and cortical terminations of the perisylvian superior longitudinal fasciculus: a fiber dissection and DTI tractography study. *Brain Struct Funct*, 218(1), 105-121. doi: 10.1007/s00429-012-0386-5
- Matchin, W., & Hickok, G. (2016). 'Syntactic Perturbation' During Production Activates the Right IFG, but not Broca's Area or the ATL. *Front Psychol*, 7, 241. doi: 10.3389/fpsyg.2016.00241
- Mesulam, M. M., Thompson, C. K., Weintraub, S., & Rogalski, E. J. (2015). The Wernicke conundrum and the anatomy of language comprehension in primary progressive aphasia. *Brain*, 138(Pt 8), 2423-2437. doi: 10.1093/brain/awv154
- Meyer, L., Obleser, J., Anwender, A., & Friederici, A. D. (2012). Linking ordering in Broca's area to storage in left temporo-parietal regions: the case of sentence processing. *Neuroimage*, 62(3), 1987-1998. doi: 10.1016/j.neuroimage.2012.05.052
- Moritz-Gasser, S., Herbet, G., & Duffau, H. (2013). Mapping the connectivity underlying multimodal (verbal and non-verbal) semantic processing: a brain electrostimulation study. *Neuropsychologia*, 51(10), 1814-1822. doi: 10.1016/j.neuropsychologia.2013.06.007
- Ono, M., Kubik, S., & Abernathy, C.D. (1990). *Atlas of the cerebral sulci*: Thieme.
- Papagno, Costanza, Miracapillo, Christiano, Casarotti, Alessandra, Romero Lauro, Leonor J, Castellano, Antonella, Falini, Andrea, . . . Bello, Lorenzo. (2011). What is the role of the uncinate fasciculus? Surgical removal and proper name retrieval. *Brain*, 134(Pt 2), 405-414. doi: 10.1093/brain/awq283
- Papathanassiou, D., Etard, O., Mellet, E., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2000). A common language network for comprehension and production: a contribution to the definition of language epicenters with PET. *Neuroimage*, 11(4), 347-357. doi: 10.1006/nimg.2000.0546 S1053-8119(00)90546-9 [pii]
- Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, 435(7046), 1235-1238. doi: nature03628 [pii] 10.1038/nature03628
- Pinker, S., & Jackendoff, R. (2005). The faculty of language: what's special about it? *Cognition*, 95(2), 201-236. doi: 10.1016/j.cognition.2004.08.004
- Poeppel, D. (2014). The neuroanatomic and neurophysiological infrastructure for speech and language. *Curr Opin Neurobiol*, 28, 142-149. doi: 10.1016/j.conb.2014.07.005
- Poeppel, D., Emmorey, K., Hickok, G., & Pyllkanen, L. (2012). Towards a new neurobiology of language. *J Neurosci*, 32(41), 14125-14131. doi: 10.1523/JNEUROSCI.3244-12.2012
- Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language. *Cognition*, 92(1-2), 1-12. doi: 10.1016/j.cognition.2003.11.001

- S0010027703002257 [pii]
- Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Ann N Y Acad Sci*, *1191*, 62-88. doi: NYAS5444 [pii]
10.1111/j.1749-6632.2010.05444.x
- Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat Neurosci*, *12*(6), 718-724. doi: nn.2331 [pii]
10.1038/nn.2331
- Rijntjes, M., Weiller, C., Bormann, T., & Musso, M. (2012). The dual loop model: its relation to language and other modalities. *Front Evol Neurosci*, *4*, 9. doi: 10.3389/fnevo.2012.00009
- Rolheiser, T., Stamatakis, E. A., & Tyler, L. K. (2011). Dynamic processing in the human language system: synergy between the arcuate fascicle and extreme capsule. *J Neurosci*, *31*(47), 16949-16957. doi: 10.1523/JNEUROSCI.2725-11.2011
- Santi, A., Friederici, A. D., Makuuchi, M., & Grodzinsky, Y. (2015). An fMRI study dissociating distance measures computed by Broca's area in movement processing: clause boundary vs. identity. *Front Psychol*, *6*, 654. doi: 10.3389/fpsyg.2015.00654
- Sapir, E. (1921). *Language: An Introduction to the Study of Speech*. New York: Harcourt, Brace and company.
- Sarubbo, S., De Benedictis, A., Maldonado, I. L., Basso, G., & Duffau, H. (2013). Frontal terminations for the inferior fronto-occipital fascicle: anatomical dissection, DTI study and functional considerations on a multi-component bundle. *Brain Struct Funct*, *218*(1), 21-37. doi: 10.1007/s00429-011-0372-3
- Saur, D. (2015). Commentary on Bajada et al., *Cortex*, in press: Transport for language south of the sylvian fissure: The routes and history of the main tracts and stations in the ventral language network. *Cortex; a journal devoted to the study of the nervous system and behavior*. doi: 10.1016/j.cortex.2015.06.004
- Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M-S., . . . Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences of the USA*, *105*(46), 18035-18040.
- Schmahmann, J D, & Pandya, D N. (2006). *Fiber Pathways of the Brain*. Oxford, England: Oxford University Press.
- Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: convergent neuroimaging and neuropsychological evidence for the function of Broca's area. *Proc Natl Acad Sci U S A*, *106*(1), 322-327. doi: 10.1073/pnas.0805874106
- Schwartz, M. F. (1984). What the classical aphasia categories can't do for us, and why. *Brain Lang*, *21*(1), 3-8.
- Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends Neurosci*, *26*(2), 100-107. doi: 10.1016/S0166-2236(02)00037-1
- Searle, J.R. (1992). *The Rediscovery of the Mind*: The MIT Press.
- Seltzer, B., & Pandya, D. N. (1994). Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: A retrograde tracer study. *Journal of Computational Neurology*, *343*, 445-463.
- Skeide, M. A., & Friederici, A. D. (2016). The ontogeny of the cortical language network. *Nat Rev Neurosci*, *17*(5), 323-332. doi: 10.1038/nrn.2016.23
- Smith, G.E. (1907). A New Topographical Survey of the Human Cerebral Cortex, being an Account of the Distribution of the Anatomically Distinct Cortical Areas and their Relationship to the Cerebral Sulci. *Journal of Anatomy and Physiology*, *41*(4), 237-254.
- Sporns, O. (2011). From simple graphs to the connectome: Networks in neuroimaging. *Neuroimage*. doi: 10.1016/j.neuroimage.2011.08.085

- Thothathiri, M., Kim, A., Trueswell, J. C., & Thompson-Schill, S. L. (2012). Parametric effects of syntactic-semantic conflict in Broca's area during sentence processing. *Brain Lang*, *120*(3), 259-264. doi: 10.1016/j.bandl.2011.12.004
- Toga, A. W., & Thompson, P. M. (2007). What is where and why it is important. *Neuroimage*, *37*(4), 1045-1049; discussion 1066-1048. doi: 10.1016/j.neuroimage.2007.02.018
- Tomaiuolo, F., MacDonald, J. D., Caramanos, Z., Posner, G., Chiavaras, M., Evans, A. C., & Petrides, M. (1999). Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: an in vivo MRI analysis. *Eur J Neurosci*, *11*(9), 3033-3046.
- Turken, A. U., & Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front Syst Neurosci*, *5*, 1. doi: 10.3389/fnsys.2011.00001
- Vogt, C., & Vogt, O. (1919). Ergebnisse unserer hirnforschung 1.-4. Mitteilung. *J. Psychol. Neurol.*, *25*, 279-461.
- Von Der Heide, R. J., Skipper, L. M., Klobusicky, E., & Olson, I. R. (2013). Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain*, *136*(Pt 6), 1692-1707. doi: 10.1093/brain/awt094
- Von Economo, C.F., & Koskinas, G.N. (1925). *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen*. Berlin: Springer.
- von Monakow, C. (1897). *Gehirnpathologie. I. Allgemeine einleitung. II. Localisation. III. Gehirnblutungen. IV. Verstopfung der Hirnarterien.* (Vol. 9(1)). Wien: Alfred Hölder.
- Wang, J., Fan, L., Wang, Y., Xu, W., Jiang, T., Fox, P. T., . . . Jiang, T. (2015). Determination of the posterior boundary of Wernicke's area based on multimodal connectivity profiles. *Hum Brain Mapp*, *36*(5), 1908-1924. doi: 10.1002/hbm.22745
- Wang, Y., Fernandez-Miranda, J. C., Verstynen, T., Pathak, S., Schneider, W., & Yeh, F. C. (2013). Rethinking the role of the middle longitudinal fascicle in language and auditory pathways. *Cereb Cortex*, *23*(10), 2347-2356. doi: 10.1093/cercor/bhs225
- Weiller, C., Bormann, T., Saur, D., Musso, M., & Rijntjes, M. (2011). How the ventral pathway got lost: and what its recovery might mean. *Brain Lang*, *118*(1-2), 29-39. doi: 10.1016/j.bandl.2011.01.005
- Wernicke, C. (1874). *Der aphasische symptomkomplex: Eine psychologische studie auf anatomischer basis*. Breslau: Cohn & Weigert.
- Wernicke, C. (1874/1969). The symptom complex of aphasia: A psychological study on an anatomical basis *Boston studies in the philosophy of science* (pp. 34-97). Dordrecht: D. Reidel Publishing Company.
- Wernicke, C. (1874/1977). The aphasic symptom complex (G. E. Eggert, Trans.) *Reprinted in Wernicke's works on aphasia: A source book and review* (pp. 91-144). The Hague, Netherlands: Mouton.
- Wernicke, C. (1881). Lehrbuch der geirnkrankeiten fur aerzte und studirende. *Kassel Theodor Fischer*, *2*, 229-242.
- Wernicke, C. (1908). The symptom-complex of aphasia. (J. L. Salinger, Trans.). In A. Church (Ed.), *Diseases of the nervous system*. (pp. 265-324). New York: Appleton.
- Wise, R. J., Greene, J., Büchel, C., & Scott, S. K. (1999). Brain regions involved in articulation. *Lancet*, *353*, 1057-1061.
- Yeatman, J. D., Rauschecker, A. M., & Wandell, B. A. (2013). Anatomy of the visual word form area: adjacent cortical circuits and long-range white matter connections. *Brain Lang*, *125*(2), 146-155. doi: 10.1016/j.bandl.2012.04.010
- Yeatman, J. D., Weiner, K. S., Pestilli, F., Rokem, A., Mezer, A., & Wandell, B. A. (2014). The vertical occipital fasciculus: a century of controversy resolved by in vivo measurements. *Proc Natl Acad Sci U S A*, *111*(48), E5214-5223. doi: 10.1073/pnas.1418503111

Zilles, K., & Amunts, K. (2012). Neuroscience. Segregation and wiring in the brain. *Science*, 335(6076), 1582-1584. doi: 10.1126/science.1221366

Zilles, K., Schleicher, A., Langemann, C., Amunts, K., Morosan, P., Palomero-Gallagher, N., . . . Roland, P. E. (1997). Quantitative analysis of sulci in the human cerebral cortex: development, regional heterogeneity, gender difference, asymmetry, intersubject variability and cortical architecture. *Human brain mapping*, 5(4), 218-221. doi: 10.1002/(SICI)1097-0193(1997)5:4<218::AID-HBM2>3.0.CO;2-6

Figures

Wernicke, 1874

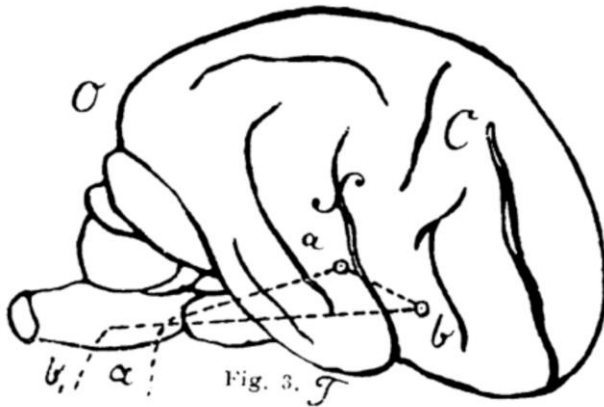


Fig. 3 [The speech areas and their connections. The "a" near the Sylvian fissure should have been designated "a,."]]

Geschwind, 1972

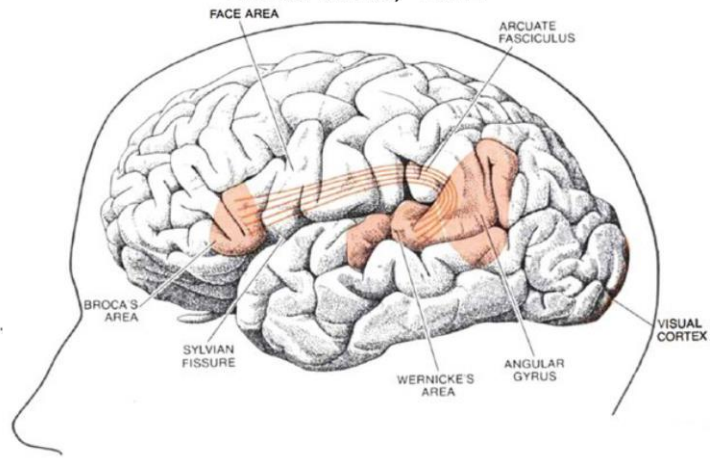


Figure 1. Left: The original model from Wernicke, 1874. For unknown reasons, the model is represented on the right hemisphere. Right: An update of the Classic model from Geschwind, 1972. In this figure, according to most anatomical definitions, the superior temporal gyrus is inadvertently mislabeled as the angular gyrus.

Percentage of respondents endorsing particular definitions of Wernicke's Area

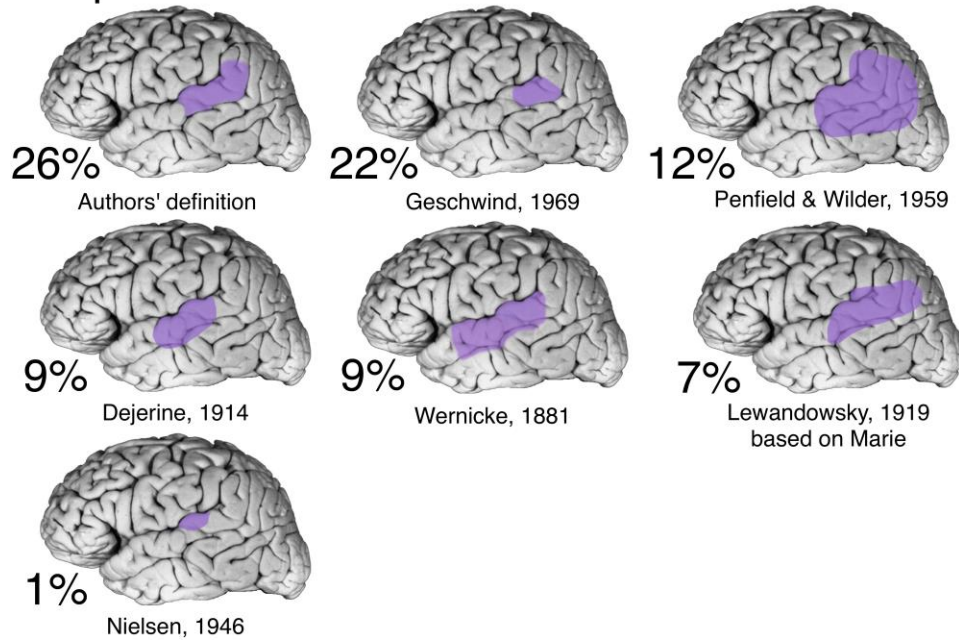


Figure 2. Anatomical definitions of Wernicke's area, and the percentage of respondents to the survey endorsing each definition. Associated citations are provided in the references section.

Percentage of respondents endorsing particular definitions of Broca's Area

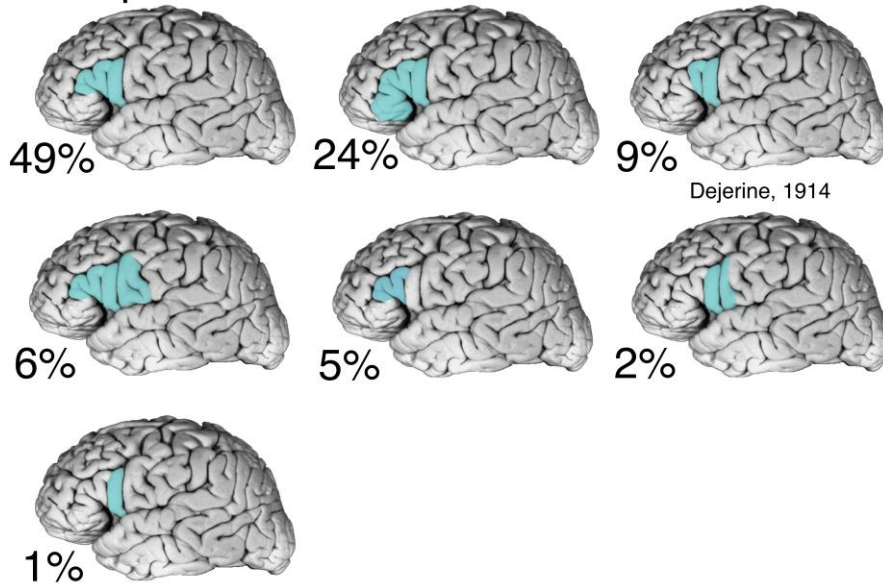


Figure 3. Anatomical definitions of Broca's area, and the percentage of respondents to the survey endorsing each definition. Associated citations are provided in the references section.

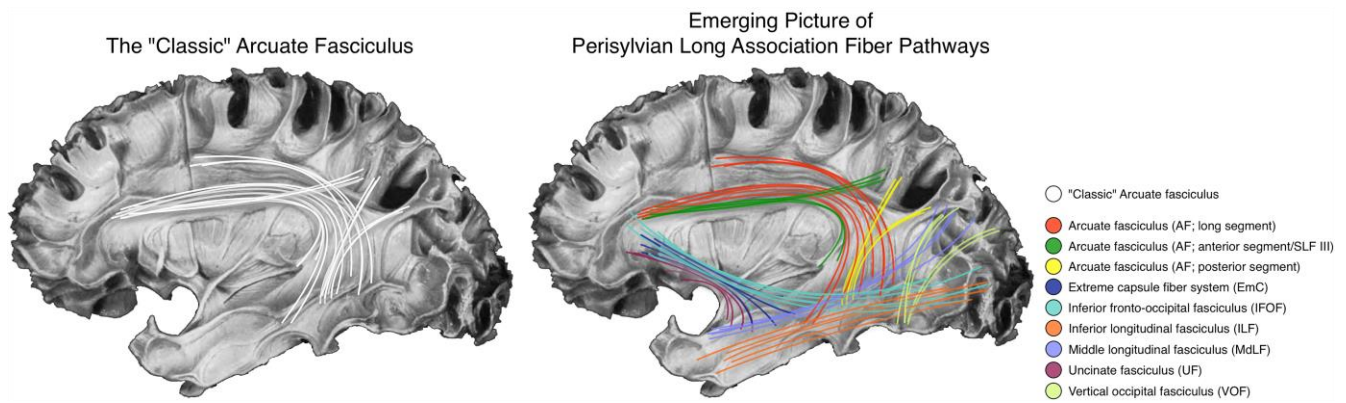


Figure 4. An emerging picture of perisylvian long association fiber pathways supporting language. The left shows the “classic” arcuate fasciculus. In the figure on the right, the arcuate fasciculus is split into three components (Catani et al., 2005). Additional fiber pathways discussed in the text are shown. SLF III = Superior longitudinal fasciculus, third subcomponent.

Frontal Aslant Tract

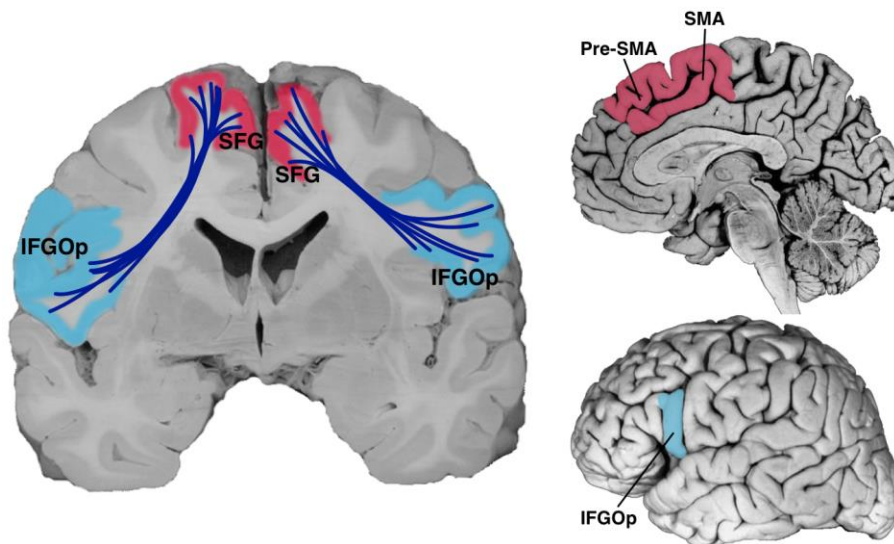


Figure 5. Connections of the frontal aslant tract (FAT) in coronal section, with outline of the inferior frontal and superior frontal origins and terminations in the medial and lateral sagittal views. IFGOp = inferior frontal gyrus, *pars opercularis*; SFG = superior frontal gyrus; SMA = supplementary motor area; Pre-SMA = pre-supplementary motor area. Reprinted with permission from Dick, A. S., Bernal, B., & Tremblay, P. (2014). The language connectome: New pathways, new concepts. *The Neuroscientist*, 20, 453-467.

Table

Table 1. Results of a literature search conducted on November 26th 2015 in two databases (PubMed and PsycINFO) using “Broca’s area” and “Wernicke’s area” as keywords in the Title and Abstract fields.

Search	PubMed results				PsycINFO results			
	Publication date				Publication date			
	2000-2005	2005-2010	2010-2015	Total	2000-2005	2010-2015	2005-2010	Total
Wernicke's area	84	86	116	286	65	72	102	239
Broca's area	247	317	374	938	186	264	291	741
Total	331	403	490	1224	251	336	393	980