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# How Localized are Language Brain Areas? A Review of Brodmann Areas Involvement in Oral Language

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**Abstract**

The interest in understanding how language is "localized" in the brain has existed for centuries. Departing from seven meta-analytic studies of functional magnetic resonance imaging activity during the performance of different language activities, it is proposed here that there are two different language networks in the brain: first, a language reception/understanding system, including a "core Wernicke's area" involved in word recognition (BA21, BA22, BA41, and BA42), and a fringe or peripheral area ("extended Wernicke's area:" BA20, BA37, BA38, BA39, and BA40) involved in language associations (associating words with other information); second, a language production system ("Broca's complex:" BA44, BA45, and also BA46, BA47, partially BA6-mainly its mesial supplementary motor area-and extending toward the basal ganglia and the thalamus). This paper additionally proposes that the insula (BA13) plays a certain coordinating role in interconnecting these two brain language systems.

*Keywords:* Language; Brodmann areas; Meta-analysis; Wernicke's area; Broca's area



## Introduction

The interest in understanding the "localization" of language in the brain has existed for centuries (Eling, 1994; Tesak & Code, 2008). This interest notoriously increased during the late 18th and early 19th centuries with the development and spread of the so-called phrenology movement (Simpson, 2005) and received a scientific anatomical impulse with Broca's (1861, 1863) and Wernicke's (1874/1970) clinical studies. During that historical moment (the second half of the 19th century), it was supposed that language was associated with the activity of three areas in the left hemisphere: the posterior frontal lobe, the upper segment of the temporal lobe, and the insula. Wernicke stated, "The whole area of the convolution encircling the Sylvian fissure, in association with the cortex of the insula, serves as speech center. The first frontal gyrus, being motor, is the center for representation of movements, and the first temporal gyrus, being sensory, is the center for word-images" (Wernicke, 1874/1970, p. 280). Dejerine (1914) integrated the available clinical/anatomical observations and proposed there was a "language area" (or "language zone") in the brain. This area included Broca's area, located in the left inferior frontal gyrus corresponding to Brodmann Area (BA) 44; Wernicke's area (posterior segment of the first temporal gyrus; BA22); and a "written language center" (angular gyrus; BA39). Although he suggested that the insula (BA13) may also participate in language, he did not explicitly include it within the brain language area. As a result, the interest in the potential participation of the insula in language virtually disappeared until the end of the 20th century. Dronkers (1996) demonstrated that the insula is a critical brain region for the coordination of complex articulatory movements (speech praxis). Further articles were published emphasizing the participation of the insula in language during the following years (e.g., Ardila, 1999; Ardila, Benson & Flynn, 1997).


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During the last decades of the 20th century, the aphasia model was generally used to illustrate the brain organization of language (e.g., Brown, 1976; Damasio, 1992; Obler & Gjerlow, 1999). That is, brain organization of language was explained departing from language pathology. Different types of language disorders were reported in cases with brain damage, depending upon the specific location of the damage. Consequently, it was proposed that specific brain areas are involved in processing particular aspects of language. Two major aphasia models were generally used during the middle and late 20th century: Geschwind and associates' model and Luria's model.

(1) Geschwind and associates' model (so-called Wernicke–Geschwind model of language) (Benson, 1979; Geschwind, 1970, 1972; Kertesz, 1985) represents an extension of the Wernicke–Lichtheim model (Lichtheim, 1885). In this model, seven different types of aphasia, each one related with the pathology of a specific brain area, are distinguished: motor, sensory, conduction, transcortical motor, subcortical motor, transcortical sensory, and subcortical sensory. Minor variations to the basic classification, proposed by Wernicke, were sometimes used (e.g., Hécaen & Albert, 1978; Lecours, Lhermitte, & Bryans, 1983). According to the Wernicke–Geschwind model, three major dimensions of language can be impaired in cases of aphasia: fluency (in cases of pre-rolandic aphasias), comprehension (in temporal lobe aphasias), and repetition (in perisylvian aphasias).

(2) Luria's model (1964, 1970, 1976). According to Luria's aphasia interpretation, seven different forms of aphasia can be recognized: efferent motor or kinetic, dynamic, afferent motor or kinesthetic, semantic, acoustic-agnosic, acoustic-amnesic, and amnesic. Each one suggests a specific level (factor) of language processing impairment. Following Jakobson's linguistic analysis of aphasia (Jakobson, 1964; Jakobson & Halle, 1956), Luria (1964) assumed that these diverse aphasic syndromes could be grouped into two major language axes or dimensions: paradigmatic and syntagmatic. Some aphasias can be due to a paradigmatic disorder (i.e., inability to select language elements), whereas others can be the result of a syntagmatic impairment (i.e., inability to sequence language elements). In pre-rolandic aphasias (motor kinetic and dynamic), the syntagmatic dimension of language is impaired (sequencing words in a sentence in the first one; sequencing sentences in language discourse in the second one); whereas the retro-rolandic aphasias are due to a defect in the selection process (selecting phonemes in acoustic-agnosic; selecting words in acoustic-amnesic; selecting the word meanings in amnesic; and selecting the meaning of word spatial relations in semantic aphasia) (paradigmatic axes of language).

During the early 21st century, Ardila (2010) further developed the idea concerning the two fundamental dimensions in language impairments. He proposed—following Jakobson linguistic analysis—that there are only two fundamental forms of aphasia which are linked to impairments in the lexical-semantic (paradigmatic axes) and grammatical (syntagmatic axes) systems of language, namely Wernicke-type aphasia and Broca-type aphasia, respectively (Ardila, 2011, 2012). He further suggested that grammar correlates with the ability to internally represent actions (verbs), depending on the functioning of what is known as Broca's area (BA44 and BA45) and its related brain circuits; it is also associated with the ability to quickly carry out the sequencing of articulatory movements required for speaking (speech praxis). He argued that lexical-semantic and grammatical systems not only depend on different brain circuitries but also on different types of memory and learning (declarative and procedural). These systems tend to appear at different moments during language development in the child and language evolution in humankind. Ardila emphasized that other aphasic syndromes do not impair language knowledge *per se*, but rather peripheral mechanisms required to produce language (in conduction aphasia and the aphasia of the supplementary motor area), or the executive control of language (in extra-Sylvian, transcortical motor, or dynamic aphasia).

The introduction of contemporary neuroimaging techniques, especially positron emission tomography and functional magnetic resonance imaging (fMRI), significantly advanced the understanding of the brain organization of language. Regardless of the diversity of methodological limitations that can be pointed out through the use of these neuroimaging techniques (Logothetis, 2008), it has become clear that language is associated with brain networks or circuits rather than with specific brain areas (Ferstl, Neumann, Bogler, & Von Cramon, 2008; Gitelman, Nobre, Sonty, Parrish, & Mesulam, 2005; Papathanassiou et al., 2000). These contemporary techniques have allowed the localization of language processing areas in the brain to be re-analyzed. Attempts have been made to pinpoint the language-comprehensive area in the temporal lobe (BA22, BA21) (e.g., DeWitt & Rauschecker, 2013; Dronkers, Redfern, & Knight, 2000; Poeppel & Hickok, 2004), as well the language production area in the frontal lobe (BA44, BA45) (Foundas, Daniels, & Vasterling, 1998; Foundas, Eure, Luevano, & Weinberger, 1998; Grodzinsky & Amunts, 2006; Grodzinsky & Santi, 2008; Ullman, 2006). For instance, DeWitt and Rauschecker (2013) suggested two different systems can be distinguished in Wernicke's area: dorsal and ventral. The left superior temporal gyrus (ventral stream) (roughly BA22) supports auditory word-form recognition, whereas the superior temporal/inferior parietal lobule (dorsal stream) (roughly BA22, BA39) supports functions of "inner speech."

There is a significantly large body of research today based on functional neuroimaging techniques. Now is the time to put these significant amounts of information collected during these last decades together, develop more meta-analytic studies to integrate and reinterpret the available fragmented pieces of information, and ultimately reach a clearer understanding of the brain organization of language.

## Contribution of Different BAs to the Language System

To further advance understanding about the brain organization of language and departing from contemporary neuroimaging techniques, a series of meta-analytic studies were recently executed (Ardila, Bernal, & Rosselli, 2014a, 2014b, 2015, in press; Bernal, Ardila, & Rosselli, 2015; Rosselli, Ardila, & Bernal, 2015). These studies aimed to analyze the specific contribution of different BAs to the language system. A meta-analytic approach integrating a significant amount of recent neuroimaging studies potentially allows an overall perspective of the different circuits and areas involved in language processing. Some areas potentially involved in language reception and understanding (lexical-semantic system) as well as areas involved in language production (grammatical system) were analyzed. Two frontal areas (BA44 and BA46) were selected. BA44 is regarded as the core Broca's area and BA46 is considered a major frontal lobe executive functioning area. In the temporal lobe, three areas surrounding the classical Wernicke's area (BA22 and BA21) were analyzed: BA20, BA37, and BA38. Because the angular gyrus (BA39) is at times included within the Wernicke's area (e.g., Mesulam, 1998), it was also studied. Finally, the insula (BA13) was notably analyzed, considering its unclear, but perhaps crucial involvement in language processes.

Brain areas co-activated when performing a particular task suggest that they belong to a common specific network or brain circuit related to the function selected as filter criterion (e.g., language). Thus, it is assumed that if two or more areas are activated within the same task they are functionally connected and consequently participate in a single network.

Currently, there are several techniques that potentially demonstrate brain circuitries or networks. These techniques are grouped under the term "brain connectivity." Recently, a new alternative approach to study brain connectivity has been proposed by Robinson, Laird, Glahn, Lovallo, and Fox (2010) known as *meta-analytic connectivity modeling* or MACM. MACM is based on automatic meta-analysis done by pooling co-activation patterns. The technique takes advantage of Brainmap.org's repository of functional MRI studies (e.g., Fox & Lancaster, 2002; Laird, Lancaster, & Fox, 2005; Van Essen, 2002) and of Sleuth, a special software provided by the same group to find, filter, organize, plot, and export the peaks coordinates for further statistical analysis of its results. Sleuth provides a list of foci, in Talairach or MNI coordinates, each one representing the center of mass for a cluster of activation. The method takes the region of interest (for instance, BA44), makes it the independent variable, and interrogates the database for studies showing activation of the chosen target. The query is easily filtered by different conditions (such as age, normal vs. patients, type of paradigm, domain of cognition, etc.). By pooling the data with these conditions, this tool provides a universe of co-activations that can be statistically analyzed for significant commonality. As a final step, activation likelihood estimation (ALE) (Laird, Fox, et al., 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002) is performed utilizing GingerALE, another software provided by Brainmap, which assesses the probability of an event to occur at voxel level across studies. As mentioned, this methodology assumes coactivation of brain areas within the same task to indicate interconnectivity between activated areas and their participation in a common network.

In the papers included in the current review, meta-analyses of seven discrete BAs were performed. The following common criteria were used: first, studies reporting activation of a specific BA (i.e., BA20, BA37, BA38, BA39, BA44, BA46, and BA13); second, studies using fMRI; third, context: normal subjects; fourth, activations: activation only; fifth, handedness: right-handed subjects; sixth, age 18–60 years; seventh, domain: cognition; subtype: language; eighth, Language: English. The final condition was used because today a significant amount of fMRI research utilizes Chinese language; including a distant language from the English phonology, lexicon, and grammar could introduce a potential uncontrolled confounding variable. The other seven conditions were used in an attempt to have a relatively homogenous normal population, studied using a single technical procedure (i.e., fMRI).

Meta-analyses of three types of brain areas were developed: first, areas involved in language reception and understanding (lexical-semantic system) (BA20, BA37, BA38, and BA39); second, areas involved in language production (grammatical system) (BA44 and BA46); and third, the insula (BA13), a brain area potentially involved in language control and coordination.

Activation foci associated to each specific area (search criteria) were obtained automatically from the Sleuth software. This automatic report lists a number of clusters defined by the center of mass (in MNI coordinates), volume in cubic millimeter, maxima intensity (peak), and neighboring BA's-peaks within 5 mm of the maxima plus and minus with respect the orthogonal coordinates. Clusters are labeled accordingly with location of maxima. These coordinates, per subject/task/paper/BA, were exported as text files (pooled results) for analysis on the following step.

Statistical significance of clusters found on the pooled-data was then analyzed utilizing the ALE method (Eickhoff et al., 2009). This step was performed with the open source software GingerALE (http://brainmap.org). ALE treats reported peaks of activation as spatial probability distributions centered at the given coordinates. ALE computes the union of activation probabilities for each voxel, allowing differentiation between true convergence of activation foci from random clustering (noise). ALE scores obtained from thousands of random iterations are used to assign *p*-values to the observed clusters of activation. Our ALE maps were threshold at $p < .01$ corrected for multiple comparisons utilizing the *false discovery rate* method. Only clusters of 200 or more cubic millimeter were accepted as valid clusters. ALE results were overlaid onto an anatomical template suitable for MNI coordinates, also provided by BrainMap.org. For this purpose, we utilized the Multi-Image Analysis GUI (Mango) (http://ric.uthscsa.edu/mango/). A mosaic of transversal-cut insets of fusioned images was obtained utilizing the same tool.

### *Language Reception and Understanding: Lexical-Semantic System*

In four different meta-analytic studies, the role of BA20, BA37, BA38, and BA39 in language was analyzed (Table 1).

BA20 (inferior temporal gyrus and anterior part of the fusiform gyrus) (Ardila, Bernal, & Rosselli, unpublished). Eleven papers, corresponding to 12 experimental conditions, and 207 participants were used in this analysis. Our results demonstrated seven clusters of activation: The first cluster (Cluster #1) included the left temporal lobe, BA20 and BA21, whereas Cluster #2 was located at the left insula (BA13) and left prefrontal BA46. Cluster #3 involved the left inferior frontal lobe (BA47) and Cluster #4 was situated in the left inferior temporal lobe (BA37). Cluster #5 was again situated in the left prefrontal cortex (BA9). The last two clusters involved the cingulate gyrus (BA30) (Cluster #6) and the left occipital gyrus (BA19) (Cluster #7).

There were few activated areas outside the temporal lobe: insula (BA13), prefrontal cortex (BA46 & BA9), cingulate gyrus (BA30), and the occipital lobe (BA19). All seven clusters were located in the left hemisphere.

BA37 (inferior temporal gyrus, fusiform gyrus) (Ardila et al., 2015). Twenty papers, with 28 suitable experiments, and 403 participants were obtained. Twelve different clusters were found, six related to the left and six to the right hemisphere. Significantly higher connectivity values, as represented by higher ALE scores, were located in the left hemisphere. BA37 presented significant connection with left inferior temporal lobe (BA20), left prefrontal cortex (BA9, BA46, BA45 and BA47), left insula (BA13), bilateral precuneus (BA7, BA19), cerebellum, and occipital areas (BA18). It was concluded that left BA37 is a common node of two distinct networks: visual recognition (perception) and semantic language functions. It is well known that BA37 is involved in lexico-semantic associations (i.e., associating words with visual percepts) (see Brodmann's Interactive Atlas). Clinical observations demonstrate that damage in the left BA37 is associated with significant word-finding difficulties (anomia) (e.g., Antonucci, Beeson, Labiner, & Rapcsak, 2008; Kraft et al., 2014; Luria, 1976; Raymer et al., 1997), impaired naming of pictures, significant amounts of semantic paraphasias, and relatively preserved word comprehension (Foundas, Daniels, & Vasterling, 1998; Foundas, Eure, Luevano, & Weinberger, 1998; Raymer et al., 1997).

*BA38 (temporal pole).* Eleven papers, corresponding to 12 experimental conditions, and 201 participants were selected (Ardila et al., 2014b). Four different clusters of activity were found: two in the left (BA38; BA13, BA22) and two in the right hemisphere (BA7, BA21). The first cluster included BA38, while the second contained the left insula (BA13) and superior temporal lobe (BA22). The last two clusters involved were the right parietal (BA7) and temporal (BA21) lobes. Seemingly, this area has two major connection pathways: one within the left hemisphere (language) and the other involving the right hemisphere plausibly participating in visuospatial and integrative audiovisual functions.

*BA39 (angular gyrus).* Eight papers, corresponding to 13 experimental conditions, and 155 participants were selected (Rosselli et al., 2015). Sixteen activation clusters made a network that included the activation of the two angular gyri (BA39), the superior right parietal lobe (BA7) and right supramarginal gyri (BA40), the left middle temporal lobe (BA21), and the frontal lobe (bilateral premotor—BA6—and left prefrontal—BA46—). BA39 functional connectivity in language tasks were observed with other regions of the left hemisphere: frontal lobe including BA6, BA9, BA44, BA46, and BA8, parietal lobe BA40, and temporal lobe BA37. Some connectivity with the limbic cortex (cingulate gyrus) was also observed. In addition, clusters of activations were observed with right superior (BA7) and inferior parietal lobe (BA40) and the right insula (BA13). One of the clusters indicated an activation of the right precuneus (BA31).

These results are in agreement with previous findings using structural connectivity techniques and support the integrative role of the angular gyrus in language functions (Binder, Desai, Graves, & Conant, 2009; Margulies & Petrides, 2013; Seghier, Fagan, & Price, 2010; Sroka et al., 2014).

Considering these studies, it can be concluded that BA20, BA37, BA38, and BA39 have a partial participation in language, specifically associating language with other types of information. They can consequently be regarded as "language associations areas." Our results suggest that regardless of BA20, BA37, BA38, and BA39 having participation in language processes, they cannot be considered core receptive language processing areas (Wernicke's area), as the contrast with clinical model findings does not support that claim. Nonetheless, these parts could be regarded as language processing marginal areas participating in an "extended Wernicke's area" or simply "Wernicke's system."

**Table 1.** Lexical-semantic system: BA20, BA37, BA38, and BA39

| | Region (BA) | *x* | *y* | *z* | Volume ($mm^3$) |
|---|---|---|---|---|---|
| BA20 | | | | | |
| Cluster #1 | L Inferior temporal gyrus (20) | −58 | −52 | −14 | 1880 |
| | L Middle temporal gyrus (21) | | | | |
| Cluster #2 | L Insula (13) | −44 | 24 | 2 | 968 |
| | L Frontal lobe (46) | | | | |
| Cluster #3 | L Interior frontal lobe (47) | −34 | 30 | −10 | 584 |
| Cluster #4 | L Inferior temporal lobe (37) | −32 | −38 | −14 | 528 |
| Cluster #5 | L Frontal lobe (9) | −44 | 8 | 28 | 432 |
| Cluster #6 | L Cingulate gyrus (30) | −12 | −56 | 16 | 248 |
| Cluster #7 | L Superior occipital gyrus (19) | −38 | −80 | 36 | 208 |
| BA37 | | | | | |
| Cluster #1 | L Fusiform gyrus (37) | −46 | −58 | −14 | 9568 |
| | L Sub-gyralgrey matter (37) | | | | |
| | L Occipital-temporal gyrus (37) | | | | |
| | L Inferior temporal lobe (20) | | | | |
| Cluster #2 | L Inferiorfrontal gyrus (9) | −42 | 8 | 28 | 7552 |
| | L Middle frontal gyrus (46) | | | | |
| | L Insula (13) | | | | |
| | L Inferior frontal gyrus (45) | | | | |
| | L Middle frontal gyrus (47) | | | | |
| Cluster #3 | L Middle frontal gyrus (32) | −4 | 14 | 48 | 2184 |
| | L Middle frontal gyrus (6) | | | | |
| Cluster #4 | L Precuneus (19) | −30 | −64 | 48 | 1872 |
| Cluster #5 | L Inferior frontal gyrus (47) | −34 | 28 | −6 | 1336 |
| Cluster #6 | R Precuneus (7) | 30 | −66 | 44 | 1304 |
| Cluster #7 | R Fusiform gyrus (37) | 46 | −60 | −18 | 1168 |
| Cluster #8 | R Occipital-temporal gyrus (37) | 52 | −68 | 2 | 824 |
| Cluster #9 | R Posterior lobe of the cerebellum & pyramid of vermix | 30 | −68 | −32 | 424 |
| Cluster #10 | R Middle occipital gyrus (18) | 34 | −86 | 8 | 400 |
| Cluster #11 | R Anterior lobe | 40 | −58 | −30 | 288 |
| Cluster #12 | L Inferior frontal gyrus | −52 | 20 | −2 | 240 |
| BA38 | | | | | |
| Cluster #1 | L Superior temporal (38) | −52 | 8 | −18 | 536 |
| Cluster #2 | L Insula (13) | −40 | 8 | −14 | 393 |
| | Lsup temporal (22) | | | | |
| Cluster #3 | R sup parietal (7) | 22 | −68 | 52 | 368 |
| Cluster #4 | R mid temporal (21) | −50 | −2 | −22 | 288 |
| BA39 | | | | | |
| Cluster #1 | R angular gyrus (39) | 36 | −62 | 42 | 2704 |
| | R sup parietal (7) | | | | |
| | R inf parietal (40) | | | | |
| Cluster #2 | R Frontal superior (6) | 4 | 16 | 48 | 1872 |
| Cluster #3 | R Insula (13) | 36 | 24 | −4 | 1792 |
| Cluster #4 | L Frontal inferior (9) | −50 | 8 | 24 | 1616 |
| | L Precentral gyrus (6) | | | | |
| Cluster #5 | L Temporal middle (21) | −50 | −58 | 30 | 1496 |
| Cluster #6 | L Fusiform gyrus (37) | −50 | 054 | −18 | 1360 |
| Cluster #7 | L Angular gyrus (39) | −32 | −56 | 44 | 1312 |
| Cluster #8 | L Frontal inferior (44, 45) | −44 | 20 | 8 | 1232 |
| | L Frontal middle (46) | | | | |
| Cluster #9 | R Head caudate nucleus | 10 | 8 | 0 | 1040 |
| Cluster #10 | R Parietal, precuneus | 6 | −50 | 36 | 952 |
| Cluster #11 | L Frontal middle (8) | −26 | 32 | 42 | 872 |
| Cluster #12 | L Inferior parietal (40) | −44 | −40 | 46 | 696 |
| Cluster #13 | L Parahyppocamal gyrus (36) | −28 | −38 | −12 | 680 |
| Cluster #14 | L Posterior cingulate gyrus (30) | −12 | −56 | 18 | 648 |
| Cluster #15 | R Precuneus (31) | 6 | −36 | 38 | 472 |
| Cluster #16 | L Frontal left (9) | −38 | 22 | 40 | 424 |

*Language Production: Grammatical System*

In two different meta-analytic studies, the roles of BA44 and BA46 were analyzed (Table 2).

*BA44 (Broca's area; inferior frontal gyrus—pars opercularis).* Fifty-seven papers, 84 experiments, and 883 participants were selected (Bernal et al., 2015). A network consisting of 16 clusters of activation were obtained. Main clusters were located in the left frontal operculum (BA44 and further, BA47), supplementary motor area (BA6), left parietal lobe (BA7, BA39), left temporal lobe (BA22), and left secondary visual areas (BA18, BA19). There were also clusters in subcortical structures including the left thalamus, left putamen, and right cerebellum (see Fig. 1). The main cluster encompasses left BA44 and its abutting areas. These are the anterior insula (BA13), the middle frontal (BA46) gyrus, and the precentral gyrus (BA6). The second cluster is located in the left pre-SMA and anterior cingulate gyrus involving BA6 and BA32. The involvement of the right anterior cingulate gyrus could be real, or most likely, an effect of the post-processing utilized to remove pixelation and aliasing of the cluster borders. This procedure, also known as "smoothing," grows the cluster, resulting in fabricated adjacent activation areas. This effect could explain the aspect of activation of the neighbor contralateral homologue anterior cingulate gyrus. The third cluster is located in the left superior and inferior parietal lobule, an area shared by BA7, BA39, and BA40. The fourth cluster involves some mirror areas of the left Broca (right BA44, right anterior insula, and right BA9), plus one subcortical structure, namely the putamen. The fifth cluster refers to the left fusiform gyrus. The sixth cluster represents the core of the receptive language area or Wernicke's area (left BA22). The next cluster in importance is located in the left thalamus. The other clusters listed in the automated report by GingerALE are the left putamen, the right parietal lobe (BA7), the occipital lobes (BA18, BA19), the cerebellum, and the right precentral gyrus (BA4). BA44 (Broca's area) has been related to language production, grammar, language fluency, and sequencing (Ardila, 2012; Grodzinsky & Amunts, 2006).

*BA46 (convexity prefrontal cortex: anterior middle frontal gyrus).* Nineteen papers, corresponding to 60 experimental conditions, and 245 participants were selected (Ardila et al., in press). Eleven different clusters of activation were found, mostly related to the left hemisphere, including BA6, BA44, BA45, BA13, BA37, BA18, BA32, BA21, BA22, and BA19. The first cluster includes the left frontal areas BA6, BA44, BA45, BA46, and BA47. That is, the whole frontal system involved in language production. Noteworthy, this as an extensive cluster with a volume approximately eight times larger than Cluster #2 and nearly 11 times larger than Cluster #3. The rest of the activation clusters are relatively small. The second cluster includes the right insula (BA13). Cluster #3 includes the left fusiform gyrus (BA37) (most likely, the activation of the culmen of the cerebellum is explained by the smoothing effect of the adjacent activation of the left fusiform gyrus). Cluster #4 includes the left fusiform gyrus (BA37), as well as its anterior extension (BA20). Cluster #5 and Cluster #6 refer to the left occipital lobe (BA18) and medial frontal lobe (32), whereas Cluster #7 corresponds to the right BA46. Additionally, Cluster #8 is located in the superior parietal lobe (BA7) and Cluster #9 corresponds to Wernicke's area (BA22, BA21). Finally, Cluster #11 refers to the left lenticular nucleus. In conclusion, BA46 plays a central role in the language production system, most likely as related to its executive control.

It is essential to observe the pattern of activation in BA44 almost encompasses entirely BA46 activation (Fig. 1). Nonetheless, first, significant connectivity of BA44 with basal ganglia (lenticular nucleus) and the thalamus was observed while second, BA46 was mostly related with other frontal areas; its connections with posterior and subcortical areas were very limited, suggesting a fundamental role in the executive control of language production.

*The Insula as a Language Coordinating System*

BA13 (insula) (Ardila et al., 2014a). Twenty-six papers, corresponding to 39 paradigms, and 522 participants were selected. Thirteen different activation clusters were found. Insula connections included not only areas involved in language production (such as the Broca's area) and language understanding (such as the Wernicke's area) but also areas involved in language repetition (such as the supramarginal gyrus) and other linguistic functions such as BA9 in the left prefrontal lobe (part of the prefrontal cortex probably involved in complex language processes) and BA37 (involved in lexico-semantic associations) (Table 3).

The first cluster includes the left claustrum (the insular subcortical gray matter). This focus extends not only subcortically but also anteriorly toward the BA9 (middle frontal gyrus in the prefrontal cortex involved in complex language processes including the use of verbal strategies in executive functions; see: Brodmann's Interactive Atlas). The second cluster includes the anterior cingulate gyrus (BA24) (involved in motor organization—motor preparation/planning, cognitive/motor inhibition—and language initiative) and left BA6 (medial frontal gyrus). BA6 includes the supplementary motor area (SMA), clearly included in language initiation and maintenance of voluntary speech production (Ardila, 2010, 2014). Thus, this second cluster suggests a participation of the insula in a brain circuit controlling verbal initiative and maintenance of speech production.

**Table 2.** Language production/grammatical system: BA44, BA46

| | Region (BA) | *x* | *y* | *z* | Volume (mm³) |
|---|---|---|---|---|---|
| BA44 | | | | | |
| Cluster# 1 | L Inferior Frontal gyrus (44) | −47 | 15 | 15 | 39,992 |
| | L Anterior Insula (13) | | | | |
| | L Inferior frontal gyrus (9) | | | | |
| | L Precentral gyrus (6) | | | | |
| | L Inferior frontal (47) | | | | |
| | L Middle frontal (46) | | | | |
| Cluster #2 | L Superior frontal (6) | −1 | 15 | 47 | 12,904 |
| | L Medial frontal (32) | | | | |
| | R Anterior cingulate (32) | | | | |
| Cluster #3 | L Superior parietal (7) | −34 | −56 | 46 | 12,184 |
| | L Inferior parietal (39) | | | | |
| | L Supramarginal gyrus (40) | | | | |
| Cluster #4 | R Inferior frontal (44) | 42 | 19 | 1 | 10,408 |
| | R Anterior Insula (13) | | | | |
| | R Inferior frontal (9) | | | | |
| | R Putamen | | | | |
| Cluster #5 | L Fusiform gyrus (37) | −43 | −55 | −16 | 5,600 |
| | L Cerebellum. Culmen. | | | | |
| Cluster #6 | L Middle temporal (22) | −56 | −43 | 7 | 4,568 |
| | L Inferior Parietal Lobule (39) | | | | |
| Cluster #7 | L Thalamus. Medial Dorsal Nucleus | −8 | −13 | 9 | 1,968 |
| Cluster #8 | L Lentiform Nucleus. Putamen | −21 | 2 | 3 | 1,728 |
| Cluster #9 | R Superior parietal (7) | 30 | −57 | 46 | 1,288 |
| Cluster #10 | L Inferior occipital (18, 19) | −28 | −89 | −2 | 1,072 |
| Cluster #11 | R Middle occipital (18) | 33 | −84 | 4 | 728 |
| Cluster #12 | R Fusiform gyrus (19) | 41 | −72 | −16 | 536 |
| Cluster #13 | L Cerebellum. Culmen. | −27 | −61 | −24 | 248 |
| Cluster #14 | R Precentral (4) | 52 | −9 | 39 | 224 |
| Cluster #15 | R Cerebellum. Declive. | 25 | −67 | −24 | 200 |
| Cluster #16 | L Superior Temporal Gyrus (22) | −61 | −15 | 6 | 200 |
| BA46 | | | | | |
| Cluster # | 1 L Middle frontal gyrus (46) | −46 | 34 | 8 | 18904 |
| | L Precental frontal gyrus (6) | | | | |
| | L Inferior frontal gyrus (47) | | | | |
| | L Inferior frontal gyrus (45) | | | | |
| | L Inferior frontal gyrus (44) | | | | |
| Cluster # | 2 R Insula (13) | 48 | 16 | −4 | 2,424 |
| | R Insula (13) | | | | |
| Cluster # | 3 L Fusiformgyrus (37) | −42 | −50 | −20 | 1,728 |
| | L Cerebellum culmen | | | | |
| Cluster # | 4 L Fusiformgyrus (37) | −52 | −48 | −2 | 1,288 |
| | L Inferior temporal gyrus (20) | | | | |
| Cluster # | 5 L Occipital (18) | −24 | −94 | −4 | 568 |
| Cluster # | 6 L Medial frontal lobe (32) | −8 | 18 | 44 | 512 |
| Cluster # | 7 R Middle frontal gyrus (46) | 50 | 30 | 18 | 488 |
| Cluster # | 8 L Superior parietal (7) | −26 | −66 | 50 | 432 |
| Cluster # | 9 L Superior temporal lobe (22) | −46 | −24 | 0 | 296 |
| | L Middle temporal lobe (21) | | | | |
| Cluster # | 10 L Middle occipital (19) | −32 | −76 | 26 | 288 |
| Cluster # | 11 L Lenticular | −26 | 14 | 2 | 256 |

Cluster #3 includes the right insula and the insular subcortical gray matter (claustrum) and indicates an integrated activity of the left and right insula. Cluster #4 refers to left BA7 (superior parietal lobe). This area of the brain participates in ideomotor praxis (Tonkonogy & Puente, 2009), motor imagery (Solodkin, Hlustik, Chen, & Small, 2004), motor learning, (Tonkonogy & Puente, 2009), language processing (Seghier et al., 2004), and temporal context recognition (Zorrilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996). Therefore, the insula is also part of the language system related to some contextual and motor learning aspects of speech.

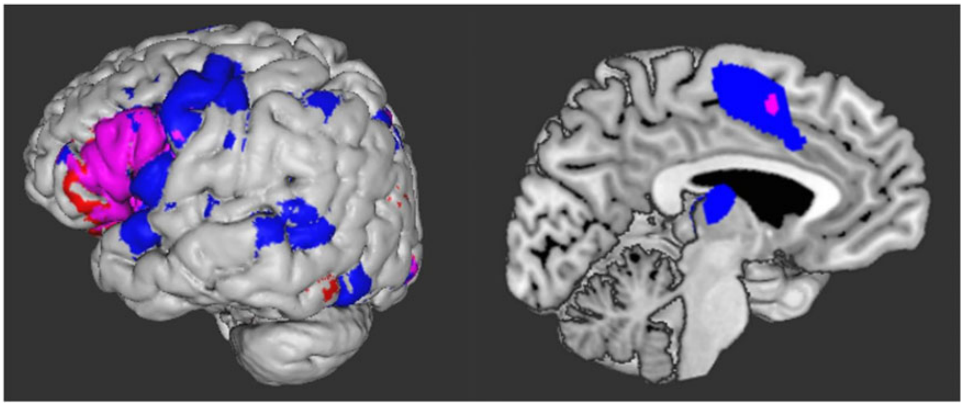

**Fig. 1.** Brain connectivity of BA44 and BA46. Left panel, left lateral view; right panel, mesial view. The networks are color coded. BA44 is represented by black and gray (blue and purple in the online version); BA46 is represented by darker gray and gray (red and purple in the online version). Hence, gray (purple in the online version) represents the shared network of BA44 and BA46. As observed, the activated areas are quite coincidental. BA46 is almost completely included within the BA44 local network which also encompasses BA45 and part of BA47. The mesial part of BA6 (pre-SMA) is largely represented within the BA44 network, sharing a small central part with BA46 connectivity. The left thalamus appears activated as part of the BA44 network. BA44 connectivity with the lenticular nucleus is not seen.

**Table 3.** The insula: language coordinating system

| | Region (BA) | *x* | *y* | *z* | Volume (mm$^3$) |
|---|---|---|---|---|---|
| Cluster #1 | L claustrum | −34 | 16 | 2 | 15,504 |
| | L insula (13) | | | | |
| | L inferior frontal gyrus (9) | | | | |
| | L inferior frontal gyrus (44) | | | | |
| Cluster #2 | L cingulate gyrus (24) | −2 | 10 | 46 | 6,672 |
| | L medial frontal gyrus (6) | | | | |
| | R cingulated gyrus (32) | | | | |
| Cluster #3 | R claustrum | 34 | 20 | 0 | 3,672 |
| | R insula (13) | | | | |
| Cluster #4 | L parietal lobe precuneus (7) | −24 | −66 | 42 | 2,720 |
| | L superior parietal (7) | | | | |
| Cluster #5 | L anterior culmen | −38 | −44 | −22 | 2,024 |
| | L fusiform gyrus (37) | | | | |
| Cluster #6 | L middle temporal gyrus (22) | −54 | −48 | 4 | 1,872 |
| | L superior temporal gyrus (22) | | | | |
| Cluster #7 | L supramarginal gyrus (40) | −44 | −40 | 42 | 1,336 |
| | L inferior parietal lobe (40) | | | | |
| Cluster #8 | L frontal precentral (4) | −50 | −10 | 44 | 800 |
| Cluster #9 | R thalamus medial dorsal n. | 10 | −16 | 6 | 488 |
| Cluster #10 | L inferior parietal lobe (40) | −54 | −24 | 36 | 400 |
| Cluster #11 | R superior temporal gyrus (41) | 46 | −32 | 6 | 320 |
| Cluster #12 | L fusiform occipital (19) | −24 | −88 | −8 | 304 |
| Cluster #13 | R cerebellum posterior lobe | 28 | −64 | −24 | 248 |

The following cluster (#5) involves BA37 (posterior inferior temporal gyrus, middle temporal gyrus, and fusiform gyrus) and the cerebellar culmen. However, considering BA37 is exactly above the culmen, this activation can most likely be referred to BA37. Consequently, Cluster #5 is suggested to only include the left BA37. The following two clusters (#6 and #7) refer to two areas traditionally involved in language: the left BA22 (superior temporal gyrus—part of Wernicke's area), and the left BA40 (supramarginal gyrus). The left BA22 is considered to be a crucial area in language understanding, whereas the left BA40 has been related to language repetition (Tonkonogy & Puente, 2009) and semantic processing (Chou et al., 2006).

The next activation clusters (#8 and #9) include the left BA4 (primary motor cortex—precentral gyrus) and the medial dorsal nucleus of the thalamus. They receive input from the hypothalamus and project to the prefrontal cortex. These clusters are known to been related to attention and memory. Although a direct relation with language is not evident, Clusters #8 and #9 may contribute to

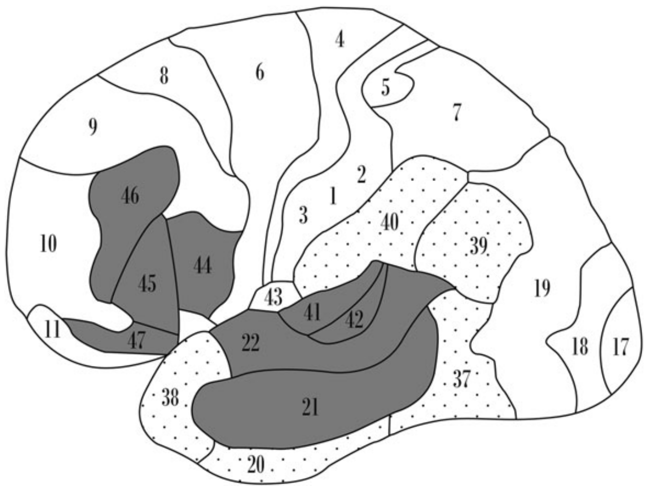


**Fig. 2.** Brain language areas. The frontal language area (Broca's complex: language production and grammar: BA44, BA45, BA46, BA47) also partially includes BA6 and extends subcortically to the basal ganglia. The posterior language area (language reception and understanding: lexical-semantic system) includes a core Wernicke's area (BA21, BA22, BA41, and BA42) and an "extended Wernicke's area" also including BA20, BA37, BA38, BA39, and BA40.

the motor aspects of speech and the attention control of language. Cluster #10 on the other hand is similar to Cluster #7 and includes the left BA40 (inferior parietal lobe). The last three clusters (notoriously smaller, with 300 $mm^3$ or less) include the BA41 (primary auditory cortex—Heschl's gyrus), the BA19 (secondary visual cortex—inferior occipital or fusiform gyrus), and the posterior lobe of the cerebellum (that could be an extension of the fusiform gyrus activation). The activation of these clusters may suggest some participation of the insula in language recognition and visual associations.

In conclusion, the insula represents a core area in language processing and it is related, not just with language production functions but also with language understanding processing. It can be conjectured that the insula is a core hub for language. Its strategic location between the anterior and posterior language areas would be crucial to play a language coordinating function.

A note of caution should be introduced. Meta-analyses give population data about brain structures involved in language but we have to keep in mind there is important inter-individual variability of cortical language representation (Dehaene et al., 1997; Ojemann & Whitaker, 1978; Tzourio-Mazoyer, Josse, Crivello, & Mazoyer, 2004). Current findings consequently refer only to populations—not individual—results.

## A Proposed Model of the Brain's Organization of Language

The above information proposes:

There is a core Wernicke's area including not only BA22 and BA21 (as usually suggested) but also BA41 and BA42.

There is a fringe, or peripheral zone, around this core Wernicke's area involved in language associations. It corresponds to BA20, BA37, BA38, BA39, and BA40 (Fig. 2). An "extended Wernicke's area" could be assumed.

In addition to the well-recognized Broca's area (BA44 and BA45), there is a complex frontal-subcortical circuit involved in language production and grammar ("Broca's complex"). It includes not only BA44 and BA45 but also BA46, BA47, partially BA6 (mainly its mesial supplementary motor area), and extends subcortically toward the basal ganglia.

The insula (BA13), probably plays a coordinating role in interconnecting these two brain language systems (lexical-semantic and grammatical).

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## References


Antonucci, S. M., Beeson, P. M., Labiner, D. M., & Rapcsak, S. Z. (2008). Lexical retrieval and semantic knowledge in patients with left inferior temporal lobe lesions. *Aphasiology*, *22 (3)*, 281–304.

Ardila, A. (1999). The role of insula in language: An unsettled question. *Aphasiology*, *13 (1)*, 79–87.

Ardila, A. (2010). A proposed reinterpretation and reclassification of aphasic syndromes. *Aphasiology*, *24 (3)*, 363–394.

Ardila, A. (2011). There are two different language systems in the brain. *The Journal of Behavioral and Brain Science*, *1*, 23–36.

Ardila, A. (2012). Interaction between lexical and grammatical language systems in the brain. *Physics of Life Reviews*, *9*, 198–214.

Ardila, A. (2014). *Aphasia handbook*. Miami, FL: Florida International University.

Ardila, A., Benson, D. F., & Flynn, F. G. (1997). Participation of the insula in language. *Aphasiology*, *11 (12)*, 1159–1169.

Ardila, A., Bernal, B., & Rosselli, M. (2014a). Participation of the insula in language revisited: A meta-analytic connectivity study. *Journal of Neurolinguistics*, *29*, 31–41.

Ardila, A., Bernal, B., & Rosselli, M. (2014b). The elusive role of left temporal pole (BA38) in language: A meta-analytic connectivity study. *International Journal of Brain Sciences, 2014*, Article ID 946039. http://dx.doi.org/10.1155/2014/946039

Ardila, A., Bernal, B., & Rosselli, M. (2015). Language and visual perception associations: Meta-analytic connectivity modeling of Brodmann area 37. *Behavioral Neurology*. *2015 (2015)*, Article ID 565871. http://dx.doi.org/10.1155/2015/565871

Ardila, A., Bernal, B., & Rosselli, M. (in press). Executive control of language: Meta-analytic connectivity modeling of Brodmann area, 46. *Psicothema*.

Ardila, A., Bernal, B., & Rosselli, M. How extended is Wernicke's area? Meta-analytic connectivity study of BA20 and integrative proposal. Unpublished.

Benson, D. F. (1979). *Aphasia, alexia and agraphia*. New York: Churchill Livingstone.

Bernal, B., Ardila, A., & Rosselli, M. Broca's area network in language functions. (2015). A Meta-analytic connectivity map based on Analysis Likelihood Estimates. *Frontiers in Psychology*, *6*, 687.

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. Retrieved January 1, 2015, from brainmap.org.

Broca, P. (1861). Remarks on the Seat of the Faculty of Articulated Language, Following an Observation of Aphemia (Loss of Speech). *Bulletin de la Société Anatomique*, *6*, 330–357.

Broca, P. (1863). Localisations des fonctions cérébrales. Siège de la faculté du langage articulé. *Bulletin de la Société d'Anthropologie*, *4*, 200–208. Brodmann's Interactive Atlas. Retrieved May 9, 2015, from http://www.fmriconsulting.com/brodmann/Introduction.html.

Brown, J. W. (1976). The neural organization of language: Aphasia and lateralization. *Brain and Language*, *3 (4)*, 482–494.

Chou, T. L., Booth, J. R., Bitan, T., Burman, D. D., Bigio, J. D., Cone, N. E., et al. (2006). Developmental and skill effects on the neural correlates of semantic processing to visually presented words. *Human brain mapping*, *27 (11)*, 915–924.

Damasio, A. R. (1992). Aphasia. *New England Journal of Medicine*, *326 (8)*, 531–539.

Dehaene, S., Dupoux, E., Mehler, J., Cohen, L., Paulesu, E., Perani, D., et al. (1997). Anatomical variability in the cortical representation of first and second language. *Neuroreport*, *8 (17)*, 3809–3815.

Dejerine, J. (1914). *Semiologie des affections du systeme nerveux*. Paris: Masson.

DeWitt, I., & Rauschecker, J. P. (2013). Wernicke's area revisited: Parallel streams and word processing. *Brain and Language*, *127 (2)*, 181–191.

Dronkers, N. F. (1996). A new brain region for coordinating A. *Nature*, *384*, 14.

Dronkers, N. F., Redfern, B. B., & Knight, R. T. (2000). The neural architecture of language disorders. *The New Cognitive Neurosciences*, *2*, 949–960.

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Hum Brain Mapp*, *30 (9)*, 2907–2926.

Eling, P. (Ed.). (1994). *Reader in the history of aphasia: From Franz Gall to Norman Geschwind (Vol. 4)*. Amsterdam: John Benjamins Publishing.

Ferstl, E. C., Neumann, J., Bogler, C., & Von Cramon, D. Y. (2008). The extended language network: A meta analysis of neuroimaging studies on text comprehension. *Human brain mapping*, *29 (5)*, 581–593.

Foundas, A., Daniels, S. K., & Vasterling, J. J. (1998). Anomia: Case studies with lesion localization. *Neurocase*, *4*, 35–43.

Foundas, A. L., Eure, K. F., Luevano, L. F., & Weinberger, D. R. (1998). MRI asymmetries of Broca's area: The pars triangularis and pars opercularis. *Brain and language*, *64 (3)*, 282–296.

Fox, P. T., & Lancaster, J. L. (2002). Mapping context and content: The BrainMap model. *Nature Reviews Neuroscience*, *3 (4)*, 319–321.

Geschwind, N. (1970). The organization of language and the brain. *Science*, *170 (961)*, 940–944.

Geschwind, N. (1972). *Language and the brain*. New York: WH Freeman.

Gitelman, D. R., Nobre, A. C., Sonty, S., Parrish, T. B., & Mesulam, M. M. (2005). Language network specializations: An analysis with parallel task designs and functional magnetic resonance imaging. *Neuroimage*, *26 (4)*, 975–985.

Goodglass, H. (1992). Diagnosis of conduction aphasia. In S. E. Kohn (Ed.), Conduction aphasia (pp. 39–49). Hillsdale, NJ: Lawrence Erlbaum Associates.

Grodzinsky, Y., & Amunts, K. (Eds.). (2006). *Broca's region*. New York: Oxford University Press.

Grodzinsky, Y., & Santi, A. (2008). The battle for Broca's region. *Trends in Cognitive Sciences*, *12 (12)*, 474–480.

Hécaen, H., & Albert, M. L. (1978). *Human neuropsychology*. New York: John Wiley & Sons.

Jakobson, R. (1964). Toward a linguistic typology of aphasic impairments. In A. V. S. DeReuck, & M. O'Connor (Eds.), *Disorders of language*. Boston: Little and Brown.

Jakobson, R., & Halle, M. (1956). *Fundamental of language*. The Hague: Moutin.

Kertesz, A. (1985). Aphasia. In J. A. M. Frederiks (Eds.), *Handbook of clinical neurology, vol. 45. Clinical neuropsychology*. Amsterdam: Elsevier.

Kraft, A., Grimsen, C., Kehrer, S., Bahnemann, M., Spang, K., Prass, M., et al. (2014). Neurological and neuropsychological characteristics of occipital, occipito-temporal and occipito-parietal infarction. *Cortex*, *56*, 38–50.

Laird, A. R., Fox, P. M., Price, C. J., Glahn, D. C., Uecker, A. M., Lancaster, J. L., et al. (2005). ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Human Brain Mapping*, *25*, 155–164.

Laird, A. R., Lancaster, J. J., & Fox, P. T. (2005). Brainmap. *Neuroinformatics*, *3 (1)*, 65–77.

Lecours, A. R., Lhermitte, F., & Bryans, B. (1983). *Aphasiology*. London: Baillere-Tindall.

Lichtheim, L. (1885). On aphasia. *Brain*, *7*, 433–484.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453 (7197)*, 869–878.

Luria, A. R. (1964). Factors and forms of aphasia. In A. V. S. DeReuck, & M. O'Connor (Eds.), *Disorders of language*. London: Churchill Livingstone.

Luria, A. R. (1970). *Traumatic aphasia: Its syndromes, psychology, and treatment*. Boston: Mouton de Gruyter.

Luria, A. R. (1976). *Basic problems of neurolinguistics*. The Hague: Mouton.

Margulies, D. S., & Petrides, M. (2013). Distinct parietal and temporal connectivity profiles of ventrolateral frontal areas involved in language production. *The Journal of Neuroscience*, *33 (42)*, 16846–16852.

Mesulam, M. M. (1998). From sensation to cognition. *Brain*, *121 (6)*, 1013–1052.

Obler, L. K., & Gjerlow, K. (1999). *Language and the brain*. Cambridge: Cambridge University Press.

Ojemann, G. A., & Whitaker, H. A. (1978). Language localization and variability. *Brain and Language*, *6 (2)*, 239–260.

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.

Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language. *Cognition*, *92 (1)*, 1–12.

Raymer, A., Foundas, A. L., Maher, L. M., Greenwald, M. L., Morris, M., Rothi, L. G., et al. (1997). Cognitive neuropsychological analysis and neuroanatomical correlates in a case of acute anomia. *Brain and Language*, *58*, 137–156.

Robinson, J. L., Laird, A. R., Glahn, D. C., Lovallo, W. R., & Fox, P. T. (2010). Meta-analytic connectivity modeling: Delineating the functional connectivity of the human amygdala. *Human Brain Mapping*, *31 (2)*, 173–184.

Rosselli, M., Ardila, A., & Bernal, B. (2015). Modelo de conectividad de la circunvolución angular en el lenguaje: Meta-análisis de neuroimágenes funcionales. *Revista de Neurologia*, *60*, 495–503.

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional subdivisions in the left angular gyrus where the semantic system meets and diverges from the default network. *The Journal of Neuroscience*, *30 (50)*, 16809–16817.

Seghier, M. L., Lazeyras, F., Pegna, A. J., Annoni, J. M., Zimine, I., Mayer, E., et al. (2004). Variability of fMRI activation during a phonological and semantic language task in healthy subjects. *Human Brain Mapping*, *23 (3)*, 140–155.

Simpson, D. (2005). Phrenology and the neurosciences: Contributions of FJ Gall and JG Spurzheim. *ANZ Journal of Surgery*, *75 (6)*, 475–482.

Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. *Cerebral Cortex*, *14 (11)*, 1246–1255.

Sroka, M. C., Vannest, J., Maloney, T. C., Horowitz-Kraus, T., Byars, A. W., & Holland, S. K., & CMIND Authorship Consortium. (2014). Relationship between receptive vocabulary and the neural substrates for story processing in preschoolers. *Brain Imaging and Behavior*, *9 (1)*, 43–55.

Tesak, J., & Code, C. (2008). *Milestones in the history of aphasia: Theories and protagonists*. New York: Psychology Press.

Tonkonogy, J., & Puente, A. (2009). *Localization of clinical syndromes in neuropsychology and neuroscience*. New York: Springer Publishing Company.

Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage*, *16 (3, Part 1)*, 765.

Tzourio-Mazoyer, N., Josse, G., Crivello, F., & Mazoyer, B. (2004). Interindividual variability in the hemispheric organization for speech. *Neuroimage*, *21 (1)*, 422–435.

Ullman, M. T. (2006). Is Broca's area part of a basal ganglia thalamocortical circuit? *Cortex*, *42 (4)*, 480–485.

Van Essen, D. C. (2002). Windows on the brain: The emerging role of atlases and databases in neuroscience. *Current Opinion in Neurobiology*, *12 (5)*, 574–579.

Wernicke, C. (1874/1970). The aphasic symptom-complex: A psychological study on an anatomical basis. *Archives of Neurology*, *22 (3)*, 2–80.

Zorrilla, L. T., Aguirre, G. K., Zarahn, E., Cannon, T. D., & D'Esposito, M. (1996). Activation of the prefrontal cortex during judgments of recency: A functional MRI study. *Neuroreport*, *7 (15–17)*, 2803–2806.