Functional and Structural Magnetic Resonance Imaging of Human Language: A Review

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1. Introduction

In this review we outline the range of functional processes involved in language comprehension and their anatomical underpinnings, including recent data on neural connectivity specifically wired for language, using magnetic resonance imaging (MRI) as main tool. A review of this type certainly implies such a large number of references that, for the sake of concision, we have selected the most outstanding and representative studies and reviews. Our interests in identifying possible cues for the evolutionary origins of language partially guided this selection; this review is actually intended as a contribution to better understand human language.

To start with, a description of language and its components appears necessary. In this regard, we will follow the proposal by Ray Jackendoff (2002), who provides one of the most comprehensive and valuable current accounts from the linguistics. Jackendoff proposes at least three structural layers in language, all of them working simultaneously in the processing of every utterance. These layers consist of a *phonological structure*, a *syntactic structure*, and a *semantic/conceptual structure*. Additionally, a number of processes -or subprocesses- coexist within each of these three structures, all of them again working simultaneously.

The phonological structure, which roughly refers to the "sounds" of language, is probably the most complex one, containing the largest number of subprocesses. The auditory-verbal nature of human language may not be alien to this complexity. The phonological structure is actually subdivided into a *prosodic* one -referring to the different intonations along the course of a general envelope covering an entire utterance- and more partial processes referring to *syllabic*, *segmental*, and *morpho-phonological* structures. These latter three structures refer to what most people would call "phonology" as such, and roughly cover the sounds of single syllables, larger word segments, and complete words, respectively.

Syntax refers to the structure of a sentence; that is, the way in which the different words or morphemes constituting a sentence are organized -most often hierarchically-, determining their mutual relationships and dependencies. The hierarchical structure achieved by syntax establishes what the main information is and its relationships with other, secondary items of information; that is, the concrete state of affairs described in an utterance in which the meaning of individual words and morphemes combine. This structure appears "desemantized", i.e., it can be entirely independent of the individual

meanings of its constituents, as in the classical example by Chomsky: "*Colorless green ideas sleep furiously*".

The semantic/conceptual structure of a linguistic utterance is probably the most central one. Indeed, the main aim of processing any linguistic message, regardless of its syntactic structure and transmission modality, is the realization of this semantic structure. This basically consists on the "meaning" of any whole sentence, that is, what it specifically means, or the idea in the mind of the speaker that she wants to elicit in the mind of the hearer. Although this information largely relies on syntax and phonology, the semantic/conceptual structure is completely independent of them –the same idea can actually be transmitted using the two other structures in many ways-. Although single words or morphemes in isolation convey semantic/conceptual information, the combination of these individual meanings by means of syntax, which in turn is achieved by means of phonology, gives place to a different, very specific meaning or semantic structure describing a concrete and detailed situation. It is not clear, however, to which extent the semantic/conceptual structure belongs to language as such, or whether it is a general process, common to other input options such as the non-linguistic interactions between the individual and her environment. In this regard, several authors still distinguish between semantic aspects specific of language and general semantic aspects common to any domain, and this distinction is particularly applicable at the level of the meaning of single words or morphemes. However, the distinction between semantics for language and general semantics appears difficult to embrace from the neural perspective, as we will see. Whatever the case, the semantic structure taps into reality, "*space* structure", i.e., the events in the real world a linguistic message refers to.

Semantics also applies to a layer not explicitly highlighted in Jackendoff's proposal but playing a significant role in language comprehension: the *discourse* level. This level refers to the situation in which two or more sentences are comprehended together, i.e., it is the semantic analysis beyond sentences. Indeed, many of the phenomena involved at this level are even less language-specific than those at the other layers or structures. In a discourse, although the hearer is attempting to get the whole comprehension of a longer message, the final picture does not depend for the most part on what is actually heard or read but, rather, on inferences and logical relationships between the ideas transmitted linguistically. These relationships are indeed extra information added by the hearer and based on her previous knowledge of the world. Although this might not be "language" as such, language would be useless if this level is not achieved.

All the processes described so far, i.e., the phonological, prosodic, syntactic, semantic, and discourse structures, may participate in sequential order –actually following this same order - or occur largely in parallel -mostly before the first 250 ms after stimulus onset (Pulvermüller et al., 2009b)-. In the literature, these two opposing views still remain. Whatever the case, the high degree of specialization and efficiency of the human brain for speech processing at all these levels is granted by most authors.

The fact that language can be transmitted using other than the auditory/verbal modality, as in the sign languages of deaf people, or, more frequently, in written form, also deserves some consideration. Consequently, a few lines in this review will be devoted to written language. Overall, most authors would agree that the linguistic machinery in the brain is largely common to any modality, with notable exceptions appearing only when specific peripheral mechanisms are engaged during the emission or decoding of a given message.

2. The sounds of language

Phonology has been less extensively studied using neuroimaging techniques than any other aspect of language. The perspective that phonology may not be as crucial in defining human language when compared to non-human forms of communication as other aspects of language, such as semantics or, particularly, syntax (Hauser et al., 2002), has probably biased the interests of the authors apart from this structure. However, human language is primarily an auditory-verbal process which, in turn, implies cerebral specializations at this level. On one hand, phonological aspects seem to be processed into specialized brain areas located within and around primary auditory ones (Brodmann Areas –BA- 41/42, Heschl's gyrus). In this regard, there is evidence of the use of extensive regions within the superior temporal gyrus largely specialized for these functions. These regions are mostly bilateral, though some degree of left-lateralization also emerges. Accordingly, a very first step in the processing of phonological information seems to be localized very dorsally in the temporal lobe, in Heschl's gyrus, where phonology would be already distinguished from non-linguistic sounds (Price, 2000). Thereafter, an antero-lateral functional gradient starting in Heschl's gyrus and progressing toward the temporal pole seems involved in further integrating heard sounds, identifying and distinguishing concrete phonological sounds such as familiar vowels against single formants (Leff et al., 2009). Additional data complete this picture by adding more ventral -middle temporal gyrus- and posterior areas of the left temporal lobe as involved as well in these functions (Specht et al., 2009).

An additional specialization for auditory language processing refers to whole words. This is known as "word-form" analysis, which means that, rather than the processing of single phonemes or longer auditory segments, what is processed and identified at this level is the overall specific sound of an entire word; a holistic analysis. There seem to be specialized cortical regions for the integration of phonological sounds into these larger and unitary sound chains, these regions corresponding to auditory association areas in the left hemisphere. A possible candidate for this process seems to be Wernicke's area. Its location next to primary auditory areas would favor such specialization. Wernicke's area is normally located in the posterior part of BA 22 within the superior temporal gyrus and sulcus (Wise et al., 2001). There are other alternatives for the location of Wernicke's area, however. Some of them spread the posterior part of BA 22 to also cover parts of BA 39 and 40 in the parietal lobe (Mesulam, 1998), whereas others locate Wernicke's area at the unimodal auditory association areas in the superior temporal gyrus just anterior to the primary auditory cortex (Démonet et al., 1992) –then covering portions that have been already mentioned here as participating in lower-level phonological analyses-. Indeed, irrespective of whether these more anterior regions can be considered or not as belonging to Wernicke's area, they have actually been claimed as the precise location for the "auditory word form area" (Cohen et al., 2004). Interestingly, however, it has been also claimed that there are no such specific cortical sites devoted to auditory word-form processing (Price et al., 2003; these authors also claim against a "visual word-form area" -see below-).

In any event, the systemic nature of the brain becomes already patent even at these very primary stages of language comprehension. In other words, the perception of speech sounds would not be limited to the temporal auditory and surrounding cortical areas, but is also significantly involving frontal cortical regions and subcortical nuclei normally implied in production (i.e., motor) processes. Accordingly, in addition to the superior temporal cortex, the most posterior portions of the left inferior frontal regions -comprising parts of Broca's

area-, the left basal ganglia, and even the (right) cerebellum, seem to play a crucial role in identifying the phonemes and sounds used during speech processing (Bozic et al., 2010). Although specific roles for these neural circuits have still to be elucidated, their involvement has been proposed as a mechanism to better process speech sounds regardless of large variability in the input, a way to internally produce those sounds as if the hearer herself were the emitter (Lieberman, 2000). Kotz and Schwartze (2010) stress that these regions, particularly the basal ganglia and the cerebellum, process timing variables crucial for speech. Overal, this is an example of the conjoint action of perceptual and motor brain systems in cognitive processing, as supported by direct evidences as the mirror neurons (Rizzolatti & Craighero, 2004).
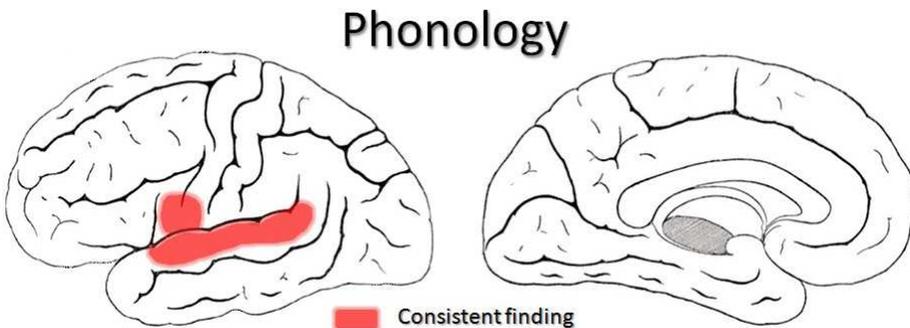

Fig. 1. Approximate locations of the phonological system

If, overall, phonology has been scarcely studied by means of MRI, the case is still worse specifically for prosody, even if this type of auditory information may be as relevant as to determining the syntactic structure of a linguistic message (Snedeker, 2008). There is evidence of the involvement of right fronto-lateral cortical areas (fronto-opercular portions in the right inferior frontal gyrus) and the right superior temporal regions in main analyses of prosody, as has been found when comparing normal speech and pseudo-speech (i.e., speech with normal prosodic intonations but devoid of known words) with degraded speech (e.g., Meyer et al., 2004). Even though, the role of the counterparts regions in the left hemisphere for the processing of prosodic information cannot be obliterated. A common circuit for language, music, and song perception comprising mid and superior temporal gyri as well as inferior and middle frontal gyri, all bilaterally, has been described (Schön et al., 2010). It is true, nonetheless, that the main implication of either hemisphere appears a function of the phonological vs. melodical nature of the input material (corresponding to left vs. right side, respectively).

3. The pictures of language

As mentioned, language can also be visual (as well as gestural), even if this is not originally the "natural" modality for human language. The human brain exhibits a high degree of flexibility and adaptability, yielding high levels of efficacy in tasks to which it is most probably not genetically prepared; reading is an outstanding example in this regard. For a long time, the place in the brain for the "visual word-from area" has been the target of strong debates, even its existence has been put into doubt (Price et al., 2003). The angular

gyrus was originally proposed as playing this role by the very first (historical) neurolinguistic models, and indeed it has appeared as such occasionally in recent functional MRI (fMRI) studies (e.g., Bookheimer et al., 1995). However, the fact that this activation is not consistent, while this region seems better characterized as semantic, has encouraged researchers to look elsewhere. A number of studies locate this functional region into Wernicke's area. But this activation is common to both visual and auditory words (Price et al., 2003) and, indeed, the most plausible functional characterization of Wernicke's area as auditory associative is difficult to conform to a visual word-form area. Some portions of the occipito-temporal cortex appear as better candidates for this function. Specifically, the most outstanding in this regard is located within the fusiform gyrus and surrounding areas -such as the lingual gyrus- in the basal temporal cortex (Dehaene et al., 2002). Interestingly, these areas would be genetically prepared for the processing of faces and objects, these functions emerging as a result of natural selection. However, by virtue of education, a portion of these regions could turn into specifically devoted to the processing of letters and visual word-forms (Dehaene, 2009).

4. The structure of language

Common to any input modality there are processes involved in understanding linguistic messages that appear of the highest interest. Syntactic processes may be among the most outstanding of these factors. As outlined above, syntax permits to determine the hierarchical structure of a sentence composed by a sequence of words (word-forms and their meanings). Studies in this regard have usually approached brain areas involved in syntactic processing using either of two procedures. On the one hand, the comparison between syntactically incorrect and correct material would enhance the activity of brain areas specialized in detecting grammatical errors. As an example, the activation during a sentence like "*the cake was eat*" is compared with its corresponding correct version. On the other hand, comparing grammatically complex sentences with simpler sentences would imply activations in areas particularly handling the complexity of syntactic structures and, hence, areas presumably involved in the hierarchical organization of the sentences. Complexity is usually increased either by embedding material within (e.g.) a main clause, rendering what is called a "recursive" structure, or by changing canonical order (usually, SVO: subject-verb-object) to a non-canonical one, as in the case of passive sentences. Examples of these situations imply comparing "*the child that my mother saw was small*" or "*the cake is being eaten by the children*", respectively, with their corresponding simpler versions (i.e., "*my mother saw a child; the child was small*", and "*the children are eating a cake*"). The case of complexity poses a problem on whether it is actually syntax what is being measured or, instead, working or short-term memory activations necessary to hold information active until the corresponding structural assignments are completed. However, it is also possible to accept that the brain areas specifically involved in working memory for syntactic structures in fact pertain to syntax processing properly, as it can be assumed that working memory for syntax implies the transient activation of circuits actually devoted to syntactic processing (e.g., Fuster, 1999; MacDonald & Christiansen, 2002).

Overall, both types of approaches to the study of human syntax have been comparable, yielding largely similar results. As one of the most consistent findings, the left inferior frontal gyrus (IFG), emerges as a central place involved in syntactic errors detection, grammatical complexity processing, and verbal working memory (e.g., Bornkessel-

Schlesewsky et al., 2009; Friederici et al., 2006; Friederici et al., 2009; Koelsch et al., 2009; Meltzer et al., 2010; Newman et al., 2009; Raettig et al., 2010; Rogalsky et al., 2008). Accordingly, the left IFG can be viewed as a main hub in the brain networks supporting syntax.

Nonetheless, IFG is a relatively extensive area, whereas syntactic rules and processes comprise a number of apparently different operations. In this regard, it seems that there are differential demands within specific portions of the left IFG as a function of the task in course. It is difficult, however, to condense the results from the different studies due to systematic inconsistencies in the criteria employed to describe their main results. In terms of Brodmann's cytoarchitectonic areas, IFG occupies, approximately -and starting from a more posterior position next to the precentral sulcus towards a more anterior one, in the left hemisphere- the most inferior portion of BA6, the whole of BA 44, the inferior half of BA 45, and BA 47 (Gray, 1918/2000; Brodmann, 1909/1994). At the same time, the IFG can be anatomically subdivided, following the same spatial sequential order as before, into the *pars opercularis*, the *pars triangularis* and the *pars orbitalis* (Gray, 1998/2000). Whereas both the anatomical and the cytoarchitectonic divisions do not match largely, some studies adopt one system but not the other, and vice versa. Several studies refine their findings by focusing on Broca's area, which certainly pertains to the left IFG. However, this is not solving the problem since there are also historical inconsistencies about what exactly are the boundaries of Broca's area. In this regard, Broca's area corresponds to BA 44 for a number of authors; for several others, BA 44, 45, and 47 should be included; for a number of other authors, the areas involved are just BA 44 and 45 (e.g., Uylings et al., 1999). Finally, in an attempt to refine anatomical exactitude when describing main results, several studies use Talairach or MNI 3D coordinates (Price, 2010). This highly precise system nonetheless obliterates the fact that fMRI is not as precise as to use these millimetrical coordinates, particularly considering the number of processing stages needed for normalization and statistical processing of the data. In addition, results in 3D coordinates usually refer to the centroid of an activated region regardless of its total size or whether its limits overlap with or surpass the anatomical or cytoarchitectonical subdivisions. In the following, we will try to minimize as far as possible these current limitations when describing the main results reported in the literature, carefully inspecting and contrasting the data reported by the different authors.

According to some reports, the most ventral part of the *pars opercularis*, roughly –but not solely- coinciding with BA 44, appears involved in verbal (syntactical) working memory (Friederici et al., 2006; Price, 2010; Rogalsky et al., 2008). In line with this might also be interpreted different results for this area as those by Bornkessel-Schlesewsky et al. (2009) for the processing of word-order variations in sentences, or Christensen (2010) and Rodd et al. (2010) for garden-path and ambiguous sentences -in which the structure must be reanalyzed and reconstructed, or several candidate structures must be kept active during sentence processing-. This ventral part of the *pars opercularis* has further been subdivided into two depending on whether the portions belong to BA 44 or to BA 6; the former would be involved in phrase structure grammar, the latter in finite state grammar (Friedrici et al., 2006). The first type of grammar refers to the use of embedded sentences, therefore demanding more working memory than the latter, simpler (linear) structures with no nesting. Detecting grammatical errors also tap on BA 44 (e.g., Heim et al., 2010), a result consistent with a role of this area in syntactic working memory to the extent that the detection of errors also increases processing demands. Overall, all these data are in line with a syntactic working memory interpretation as a main role of BA 44 (or the anterior ventral

pars opercularis). However, if we approach working memory in the sense mentioned above – i.e., that it consists of the transient activation of circuits devoted to accomplish specific operations- then BA 44 might be better seen as containing core circuits for syntactic processing determining the hierarchical syntactic structure of a sentence. This would harmonize with the variety of different syntactic operations that have been seen to tap on this area, as outlined above. In sum, BA 44 seems a central place for syntax in the brain.

The dorsal portion of the *pars opercularis* (overlapping with the most superior part of BA 44 and a portion of BA 9) appears also involved in the processing of syntactic complexity, even when working memory is factored out (Makuuchi et al., 2009). In this regard, however, it has also been claimed that this cortical region is involved in hierarchical ordering of sequences of events regardless of whether they are linguistic or not, as it has been seen to sequence (e.g.) colored shapes or nonlinguistic visual symbols (Bahlmann et al., 2009; Tettamenti et al., 2009). Its language-specificity, therefore, appears challenged. As we will see below, this is also the case for most, if not all of the areas involved in language.

This is in fact the case of BA 44 or the ventral portion of the *pars opercularis* described earlier. Tactile imagery (Yoo et al., 2003), word and face encoding (Leube et al., 2001), object manipulation (Binkofki et al. 1999), smelling familiar odors (Ciumas et al., 2008), or music enjoyment (Koelsch et al., 2006), among several others, are tasks in which BA 44 has been seen importantly involved. Moreover, and within the frame of language, even the role of BA 44 as exclusive for syntax processing does not appear to be proved. In this regard, semantic and articulatory (phonological) processes have been seen to tap also on this area (see our previous section for phonology and the next one for semantics). Possibly, these data might be understood if we assume the proposal of a functional gradient along the whole left IFG, in which -using Brodmann's areas as reference, and from left to right- BA 47 and 45 would appear mainly involved in semantic unification, BA 45 and 44 in syntactic unification, and BA 44 and ventral BA 6 in phonological unification (Hagoort, 2007). Unification is, in the end, the main defining purpose of syntactic operations: unify or "put together", according to the hierarchical structure of the sentence, the different constituents of a sentence. As the posterior part of BA 44 has been seen involved in articulation/phonology and the anterior part in semantics, it might appear that BA 44 is relevant for both phonology and semantics; or, rather, for something in between, maybe what we properly call "syntax". It might also be the case –we are here certainly speculating- that what we call syntax is indeed an abstraction that actually relies on both phonology and semantics. As can be seen, studying language with fMRI gives rise to core questions on the very nature of human language.

In this regard, the role of BA 45, roughly coinciding with the *pars triangularis* of the IFG, might also appear ambiguous. As has been just-mentioned, it seems involved in analyzing the semantic structure of the sentence. Several studies comparing sentences containing semantic anomalies with their correct counterparts (Kuperberg et al., 2008), or sentences with and without semantic ambiguities (Davis et al., 2007), consistently report activations in BA 45. But this area also appears particularly involved in analyzing embedded structures (Shetreet et al., 2009), which can be considered as a more genuine syntactic process. In line with this, BA 45 has also been seen to support the syntactic constituent structure of the sentence, in a study in which syntactic and semantic structures were disentangled (Pallier et al., 2011). In this latter study, the activation of BA 45 in *pars triangularis* spread also to IFG *pars orbitalis*, therefore including BA 47. However, it is a consistent finding the role of BA 47 in semantic processing (e.g., Binder et al., 2009; see also our section below). In sum, and as an eclectic solution, it might be possible that the most posterior part of BA 45 is relatively

more syntactic in nature, conforming a somehow unitary system together with part of BA 44; the anterior part, in turn, would be more semantic, working together with BA 47. Overall, the above-mentioned functional gradient within the left IFG might actually be more gradual than the labels currently available to describe it (i.e., semantic, syntactic, and articulatory/phonological), which might also explain why the ventral portion of BA 6, most consistently described as an articulatory/phonological area (it actually belongs to the premotor cortex) has also been seen occasionally involved in detecting syntactic errors or analyzing syntactically ambiguous sentences (Christensen, 2010; Friederici et al., 2006). The picture can be yet more complicated when considering that even language processing at the discourse level consistently recruits large portions of the IFG, as we will see below.

Additionally, a number of studies also support the involvement of other regions apart from the IFG in syntactic processing. One of the most consistent findings in this regard is the existence of a fronto-temporal network supporting syntactic processing. Whereas the frontal pole of this network implies the left IFG, especially in and around BA 44, the temporal portion is mainly comprising the left superior temporal gyrus (STG) and superior temporal sulcus (STS), most likely excluding primary auditory areas (i.e., BA 41 and 42), and roughly corresponding to BA 22 (Christensen, 2010; Rodd et al., 2010). Interestingly, these activations may plainly include Wernicke's area (Shetreet et al., 2009), which is mainly involved in the processing of language sounds (see our previous section in this regard). In several studies, large (anterior and posterior) portions of BA 22 appear relevant in syntactic processes (Friederici, 2002; Rodd et al., 2010). In other occasions, however, it is only a small portion of BA 22 what is involved, such as the posterior portion of the STS (Pallier et al., 2011). Upper portions of the middle temporal gyrus (MTG), comprising part of BA 21, have been also reported to participate in syntactic processing (Christensen, 2010; Friederici et al., 2006; Shetreet et al., 2009). Interestingly, although the main findings are located within the left hemisphere, occasional activations in corresponding areas of the right hemisphere are also reported. Several studies also report activations in the ventral portion of the supramarginal gyrus (SMG, part of BA 40), together with the *planum temporale*, a posterior portion of BA 22 (Raettig et al., 2010), although these regions appear more consistently as rather semantic, particularly the SMG (Binder et al, 2009).
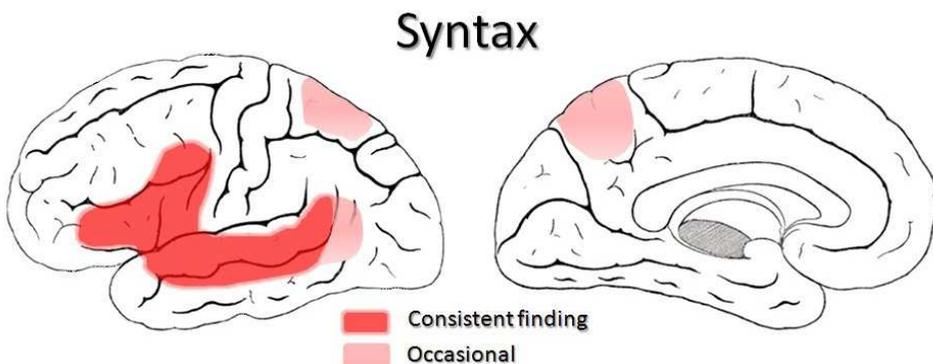

Fig. 2. Approximate locations of the syntactic system

Finally, still other brain regions have been seen also involved in syntactic processing, though less consistently. Among these, we can mention the precuneus (in the medial

parietal lobe), small portions of BA 37 (next to BA 22), superior parietal cortex (BA 7), as well as the lentiform and the caudate nuclei (e.g., Chistensen, 2010; Friederici et al., 2006; Shetreet el al., 2009).

5. The meaning of language (I)

Linguistic messages normally tell something about the world and its components (objects, persons, places, and so forth). As such, a linguistic message includes words (word-forms with their individual semantic contents or meanings) that are combined, usually through syntax, rendering a concrete description of their relationships intended to mirror a real situation or an idea. Within the brain, indeed, extensive regions of the cerebral cortex appear devoted to semantic information processing. This seemingly provides a clue on the relationships between language and other cognitive processes. But it also poses some doubts on the boundaries between what can be labeled as "linguistic" and "non-linguistic". It is also the case that "semantic" might appear as a rather vague and imprecise term, covering a large number of otherwise different processes or operations. In fact, terms as "pragmatic", "conceptual", as well as several others, often appear next to "semantic" as equivalent or corresponding to a somehow unitary system.

Actually, the meaning of words, one of the main features that the term semantic can refer to, can be just about anything in the world. In other words, human languages have words –and, then, meanings- for absolutely all (or almost all) things known so far in the world, be they real, imagined, or with a large amount of ambiguity and abstraction (e.g., Pinker, 2007). In this regard, some authors even think that the so-called "syntactic words" (i.e., complements, determiners, suffixes, and so many words or particles with a specific syntactic function) have also a meaning to be considered as plainly pertaining to the same semantic system of the brain as any other type of content word, such as nouns or verbs. In this line, it could be the case that syntactic regions reviewed above might be part of the "semantic" system, but only the part preferentially dealing with abstract structural hierarchical relationships between a number of items, be they words or whatever. Indeed, it is a plausible scenario that syntax words emerged initially as any other, less functional words during the evolution of human language (Heine & Kuteva, 2007).

This said, it should not be surprising that semantic areas have been proposed to occupy most of the cerebral cortex. Providentially, Binder et al. (2009) have recently published an extensive review of functional neuroimaging studies of semantic processing, in which not only strict inclusion criteria were applied but also advanced statistical analyses for determining the probability of a given region as belonging to the semantic system. The studies included in that review used words as stimuli, so that we can be certain that the areas suggested as supporting the semantic system are indeed areas activated by language. This note is important because, as we will see, the areas constituting the semantic system are actually and for the most part classically considered as heteromodal association areas of the neocortex, located both in frontal and posterior regions. They are therefore common to a large amount of non-linguistic processes involved in either perception or action. Additionally, areas of the limbic system involved in emotional processing are also part of the semantic system.

According to the review by Binder et al. (2009), the semantic system in the brain can be subdivided into three main widespread locations. A first one includes large portions of the posterior multimodal and heteromodal cortex, namely the angular gyrus (AG, in BA 39), the

SMG, and the MTG, including part of the temporal pole (comprising small parts of BA 38 and 29). Also in the posterior parts of the brain other areas highly involved in semantics are basal temporal areas, particularly within the fusiform and parahippocampal gyri (comprising portions of BA 20 and 37; mainly high-order visual regions, as we saw for reading). A second location of the semantic system comprises portions of the heteromodal frontal cortex, namely the upper and –especially- medial portions of BA 8 and part of BA 9. Interestingly, BA 8 contains the supplementary motor area (SMA) and has been seen involved in a variety of tasks, including motor learning and imagery (Malouin et al., 2003; Matsumura et al., 2004), executive functions and planning (Kübler et al., 2006), and even speech motor programming (de Waele et al., 2001). On the other hand, BA 9 is also involved in executive functions (e.g. Kübler et al., 2006) and, as we will see below, in discourse processing. Another frontal heteromodal association area included in the second locus of the semantic system is BA 47 in the IFG, an area that was already mentioned in our previous section on syntactic processing, its most probable function being related to semantic/pragmatic unification. Finally, the third group of areas supporting the semantic system according to Binder et al. (2009) includes the posterior cingulate/precuneus region and the ventromedial prefrontal cortex. Whereas the former has been seen to be associated with emotional processing (Maddock, 1999), it has also been related to visuospatial memory and imagery (Burgess, 2008; Epstein et al., 2007), among several other functions, including – occasionally, as we saw- syntax. Indeed, the role of this area seems rather polyvalent; later on, we will see that it is implicated in the semantic analysis of whole sentences and longer language emissions (discourses). The ventromedial prefrontal cortex, roughly corresponding to BA 11 and other BAs (such as portions of the most ventral parts of BA 10, 24, 25, and 32), comprising the rostral part of the anterior-ventral cingulate, is linked to motivation, emotion, and decision making involving reward (e.g., Ernst et al., 2004), among several other functions such as olfaction (Royet et al., 1999).

It must be remarked that all the regions outlined so far in Binder et al. (2009) as constituting the semantic system are mainly and preferentially in the left hemisphere, in consonance with the fact that they were circuits activated by words. This in turn harmonizes with the left-lateralization of other linguistic functions, such as syntax and phonetics. Overall, it seems that the semantic system activated by words largely overlaps with the system used by our brain to understand and process, as well as to interact with, the external world. In fact, this is what language crucially conveys in the very end. We have seen that words can activate association areas involved in action planning, perception, and emotions, and certainly the meaning of words ultimately refers to any of these things, or to a combination of them. However, it is also possible that the view of the semantic system sketched by Binder et al. (2009) is to some extent a restrictive one. Indeed, interactions with the external (or internal) reality imply not only heteromodal association areas, but also more primary areas. Actually, the brain areas directly supporting body movements or first stages in the perceptual processing might also be part of our semantic system. This is the idea endorsed by Pulvermüler and colleages (e.g., Pulvermüler, 2010; Pulvermüller, & Fadiga, 2010). An overview of fMRI evidences in this regard by these authors (e.g., Boulenger et al., 2009), as well as by other groups (e.g., Martin & Chao, 2001; Tomasino et al., 2007) can be summarized as supporting that words referring to concepts in which movements or actions are crucial (e.g., tools, as well as many verbs), activate cortical areas specifically devoted to directly perform those movements or actions. When the words refer to arm movements (e.g., "catch"), leg movements (e.g., "run"), or face movements (as any facial expression, like

"smile"), they activate corresponding areas for these actions within the primary motor cortex (BA 4), also largely respecting its somatotopic organization. The same is the case for words referring to specific stimulus features, or in which these features are crucial in their definition. Words such as "ellipse" or "red", or words belonging to semantic categories in which visual features prevail (like "animals"), activate visual areas specifically related to the processing of those perceptual features. Binder and colleagues, in their 2009 review, mention this type of findings, but consider them as secondary, less conspicuous and consistent than the other regions substantiating their proposal. It is possible, nonetheless, that the participation of these primary regions in the semantic system of the brain is less systematic namely because they refer to very specific actions or perceptions, so that only the linguistic material referring to these very concrete body features would activate them. This would not be the case, however, of the heteromodal and multimodal association areas, the main areas according to Binder et al. (2009) review, which by definition would be activated by any stimulus of any modality. This depiction is supported in Pulvermüller et al. (2009a).

By considering the semantic system as composed by both heteromodal and multimodal association areas as well as by primary or secondary areas of the perceptual and motor systems extends the size of the semantic system and is a very plausible scenario. Under this perspective, the semantic system would be substantiated by the cortical circuits involved in all of our interactions with the world; the semantic system would be equivalent to our whole "world knowledge" system. Part of this knowledge is concrete, but also part of it refers to abstractions and relations performed in the heteromodal and multimodal association areas. The involvement of limbic regions in the semantic system also fits with this line of reasoning, since emotions are also an important part of our world knowledge. Indeed, this depiction harmonizes well with recent theories of "embodied language" (e.g., de Vega et al., 2008), according to which language directly and straightforwardly makes use of the brain areas involved in performing or processing what is described in an utterance. Embodied language theories contrast with traditional proposals for a more "abstract" code created by language (or from which language emerges, in case of production) that can in turn be converted into the mental representation of specific perceptions and actions. Both views could complement each other, however, if both abstract and "body" codes working simultaneously and in cooperation are accepted. The former would be related to heteromodal and multimodal association areas, the latter to more primary or secondary areas. Indeed, not all that can be uttered can be visualized or executed externally. We can also add that there is a noticeable overlap between the most abstract and heteromodal portions of the semantic system -i.e., the proposed by Binder et al. (2009)- and part of the so-called "human default system", a rather bilateral network of activations in the human brain appearing when the subject is involved in mental tasks other than those linked to externally present stimuli or tasks. The fact that the human default system is involved in such a variety of mental operations as autobiographical memory, envisioning the future, theory of mind, or moral decision making, among many others (for a good review, see Buckner et al., 2008), suggests that this system can eventually apply to circumstances that can be visualized or externally performed. If we apply the same reasoning as we did above for the semantic system, the parallelisms between both systems are more apparent, as situations supported by the human default system should also involve the occasional recruitment of more primary or secondary perceptual or motor cortical areas in order to imagine specific perceptions and actions. This is a very plausible scenario (see, e.g., Kosslyn & Thompson, 2003 for fMRI evidence of primary visual areas activated in visual imagery).

The main purpose of language comprehension is nevertheless not the understanding of single words within a given utterance, but rather the specific relationships between those words. Helping to determine these relationships is the main role of syntax, which in turn contributes to elucidate the semantic structure of the sentence. The latter is a semantic frame representing the actual relationships between the different entities (objects, persons, places, and so on) mentioned in a sentence. Brain activations related to these combinatorial or propositional semantic processes are normally obtained in experiments in which grammatically correct but semantically incongruent sentences are compared with semantically congruent or plausible sentences. As an example, compare "*She spreads the warm bread with shoes*" and the same sentence ending with "*butter*" instead. In other occasions, the activations produced by normal sentences have been compared with the activations produced by sentences composed of pseudowords, or "jabberwocky" sentences, in which a syntactic structure can still be determined but -given that pseudowords have no semantic content as they are not real words-, no semantic structure can theoretically be extracted. As an example, here is a portion of the poem by Lewis Carroll that gave birth to the name of this type of paradigm: "*Twas brillig, and the slithy toves / Did gyre and gimble in the wabe; / All mimsy were the borogoves, /And the mome raths outgrabe*". Overall, the activations observed with these experimental paradigms tap on several places within the "more general" or heteromodal semantic system for words commented so far. Two of these places locate within the parieto-temporal junction and the temporal pole (Mashal et al., 2009; Obleser & Kotz, 2010; Pallier et al., 2011), that is, two portions within the posterior heteromodal association areas of the system used for words. Another portion of the semantic brain system for words that seems also importantly involved in the combination of semantic information is the posterior cingulate/precuneus (Mashal et al., 2009; Whitney et al., 2009). Finally, an area within the IFG belonging to the frontal heteromodal association areas of the semantic system -BA 47, eventually spreading to BA 45-, has also been seen implied in combinatorial semantic operations (reviewed in Hagoort, 2007). As can be seen, most of these loci have been implied in the processing of the semantic content of words; a few of them (BA 45, posterior cingulate/precuneus) have been occasionally observed in syntactic operations as well (particularly BA 45; see above). Interestingly, several of these regions also play a relevant role in discourse processing, as we will see in the next section.
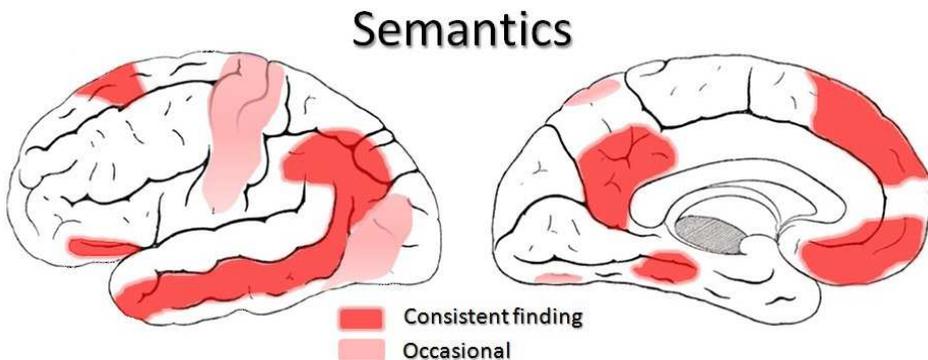

Fig. 3. Approximate locations of the semantic system

6. The meaning of language (II)

Human language normally extends beyond sentences, most often consisting of longer messages usually known as discourses, narratives, stories, or –simply- texts. The global or unitary comprehension of a group of sentences would involve even more associative areas than simpler levels, namely because additional processes, known to demand higher levels of association, play a relevant role in discourse comprehension. Among these additional processes, the most outstanding appear to be the achievement of *inferences* and *pragmatic interpretations*, obtained by using world-knowledge and discourse context constantly in interaction. Finally, according to the so-called "situational models" (Zwaan, 2004), it is also assumed that reading or hearing long linguistic messages or discourses conveys, when feasible, the recreation of the situation depicted in the text, normally by simulating or recreating the events described in the story. Results from the fMRI studies reported so far in this topic seem to support this overall depiction.

Experiments studying text comprehension have been very varied in their designs and procedures. In principle, whenever we have two or more sentences, the same processes presumably involved in text comprehension should be already in play, as linking two sentences would be sufficient to activate inferential and interpretive processes. Accordingly, if two sentences, as "*The telephone was ringing*" and "*My brother wanted to tell me the news*", are uttered consecutively, one understands that the second is an idea related to the first sentence; in this case, that it is my brother who was calling, and that the reason for his call was that my brother wanted to tell me something of interest. Without these inferences, performed easily and automatically and based on our world-knowledge, the two sentences would be just two senseless isolated emissions. A good example of the study of the coherence we normally achieve during text comprehension is extracted from Ferstl and von Cramon (2001), where coherence was compared with cohesion, that is, the linkage of two sentences by means of a cohesive element as "*therefore*" in the following pair of sentences: "*Mary's exam was about to start. Therefore, her palms were sweaty*". These two sentences are cohesive, due to the presence of a linking element, as well as coherent, since our world-knowledge tells us that sweaty palms are a possible consequence of being nervous, the latter being a normal consequence of an examination situation. In fact, both sentences are coherent even without the cohesive element. Now read the following pair of sentences: "*Mary's exam was about to start. Therefore, the pizza arrived*". Even with the cohesive element, these two sentences are not coherent; our knowledge of the world cannot help us to infer a possible logical link between these two utterances.

In other occasions, discourse processing has been studied using loosely structured passages rendered coherent only by providing a title or an illustration. As a good example, consider a portion of a classical ambiguous paragraph from Bransford and Johnson (1972): "*A newspaper is better than a magazine. The seashore is a better place than the street. At first it is better to run than to walk but walking is fine after a while. You may have to try several times, it takes skill but it's easy to learn. Even young children can enjoy it. Once successful there are very few complications. Birds seldom get too close. […]*". This paragraph is noticeably better understood - and remembered- when preceded by the title: "*Making and flying a kite*". Comparing the processing of this type of paragraphs preceded by the title and the same paragraphs without the title would yield, for the former, the activation of brain areas supplying global coherence and, for the latter, the attempts to attain it (Martín-Loeches et al., 2008).

Two recent reviews by Evelyn C. Ferstl and colleagues (Ferstl, 2010; Ferstl et al., 2008) -the first one using similar statistical methods as in Binder et al. (2009) for the semantic system-

provide an unbeatable account of the topic. Overall, and interestingly, the main results suggest that most of the areas supporting discourse comprehension overlap with the semantic system activated by words (see above), also comprising regions used as well for other more basic linguistic processes. There also exist brain regions specific for discourse processing, a remarkable finding that will be discussed later in detail.

The reviews by Ferstl et al. (2008) and Ferstl (2010) outline a number of results that could –in our view- be grouped into four principal regions. One of the most consistent findings appears to involve the anterior temporal lobes, bilaterally, particularly the temporal poles. As mentioned, this is part of the semantic system for words proposed by Binder et al., (2009), and we have seen it is also involved when sentences have to be interpreted semantically. Nonetheless, a remarkable particularity is that in discourse processing both anterior temporal poles, bilaterally, are involved whereas semantics for words was rather left-lateralized. Another distinctiveness is that the area of the anterior temporal poles involved in discourse processing is larger than the portion used for words, the former spreading ventrally and dorsally covering the whole temporal poles. Accordingly, the anterior temporal lobes, and especially the temporal poles, seem crucial for understanding the meaning of words, sentences, and paragraphs, seemingly constituting a main hub of the semantic system used in language processing. Fertl et al. (2008) propose that a main role for this area in *propositionalization*, the process required for combining words into semantically based content units. Together with the temporal poles, discourses seem also to consistently activate other region that is also crucial for word and sentence semantics: the parieto-temporal junction. This is yet a portion of the posterior heteromodal association cortex already clustered with the temporal poles when we reviewed sentence semantics.

A second group of results would comprise the left IFG and STS/STG, spreading to part of the MTG. Ferstl et al. (2008) suggest that at least part of this "fronto-temporal network", substantiate language perception, integration, and interpretation. On the other hand, these activations are not present in a number of studies, being therefore less consistent than other areas contributing to discourse processing. As we have seen earlier, the left IFG seems to exhibit a functional gradient in language processing where syntax appears to be central but phonological and semantic processes are also importantly present; additionally, the role of the STG in syntax analysis is also a consistent finding, but again phonological processes are also observed in this region. Accordingly, even if activated during discourse processing, the role of these perisylvian areas might be not so specific of longer texts. However, this issue may still need further clarification. Recent studies of very slow brain blood flow fluctuations (around 0.1 Hz) have shown that regions in the posterior part of the left superior temporal sulcus/gyrus are consistently correlated at these frequencies with left IFG, particularly within BA 44 or the *pars opercularis* (Lohman et al., 2010). This type of fluctuations might thus reflect processes clearly beyond sentences, in the range of discourse or very large language emissions. The role of these very slow fluctuations for overall language comprehension is still unknown, but the fact that this fronto-temporal network participates, to a larger or a lesser degree, in apparently all the language processes studied so far (even if mainly in phonological and syntactic) emerges as a revealing cue to better understand human language and its possible evolutionary origins.

A third group of findings outlined in Ferstl et al. (2008) and Ferstl (2010) reviews relates to mid-parietal areas, namely the posterior cingulate/precuneus. Acccordingly, apart from participating in syntactic analysis (though very occasionally) and semantics of words and sentences, this region appears of relevance for discourse processing. Indeed, this is a very consistent finding.

The fourth and last region involved in discourse processing comprises the fronto-medial prefrontal cortex (dorso-medial and ventromedial prefrontal cortex), including large portions of the medial side of BAs 8, 9, 10, and 11. To some degree, all of these areas have been mentioned before as mainly implied in the semantic analysis of words. Even though, this grouping here is somewhat different. The main divergence is that the system comprising these areas for discourse processing complements with substantial additions of neural tissue. One addition is the involvement of the entire BA 10, including not only the medial parts, but also the lateral parts -even spreading to BA 46-, which was not the case in word semantics. The other addition conveys the whole anterior cingulate gyrus (in semantics for words, only a very small ventral anterior portion of this gyrus appeared involved). The involvement of these additional portions in discourse processing may convey important consequences. First, BA 10 is the largest cytoarchitectonic area in the human brain, having increased its size substantially during human evolution, as is the case for its connections (Semendeferi et al., 2001). Second, most of these connections seem to affect the anterior cingulate particularly (Allman et al., 2002), which is another milestone in human brain evolution. In fact, the anterior cingulate is so peculiar in the human brain that it is the main structure containing a special type of neurons, the spindle or Von Economo cells. Only the great apes within the primate order posses this type of neurons presumably related with complex social behaviour, humans exhibiting a disproportionate larger number of them (Allman et al., 2011). Third, BA 10 has recently revealed as the single region showing a significant effect unique to *g*, the psychometric construct of *general intelligence* (Gläscher et al., 2010). Consequently, although this is a group of areas directly involved in language processing, its language-specificity does not appear evident.

The same appears to be the case of the posterior cingulate/precuneus region, the third group of findings involved in discourse processing. The concrete role of the posterior cingulate/precuneus has yet to be elucidated. This region participates in many linguistic processes, but also in a number of other non-linguistic operations. As mentioned earlier, it appears a certainly polyvalent region, involved in emotion, memory, and imagery; it also belongs to the human default system, and it is one of the very few regions connected reciprocally with most other cortical regions. Indeed, this part of the brain is one of the main hubs of the "human core system", the anatomical counterpart of the human default system (Chudek et al., 2008). On the other hand, the anterior medial regions also involved in discourse processing are again largely overlapping with corresponding portions of the human default system. This outstanding overlap between brain systems for word semantics and, particularly, discourse processing and the human default system has been already raised by Binder et al. (2009) and Speer et al. (2009). Ferstl et al. (2008) and Ferstl (2010) focused on the similarities of the discourse-processing system and the system supporting theory of mind. However, considering that the circuits for theory of mind and the human default system have been seen to be largely equivalent (e.g. Buckner et al., 2008), Ferstl and colleagues' suggestion could surely be reworded to imply the default system. Overall, the human default system appears to be such a general and abstract-coded system that it can apply to a considerable number of situations and circunstances, including word semantics and discourse processing in language. Eventually, the recruitment of more primary and secondary perceptual or motor areas would also be necessary in order to visualize or imagine specific perceptions, actions, or any type of situations outlined in a text.
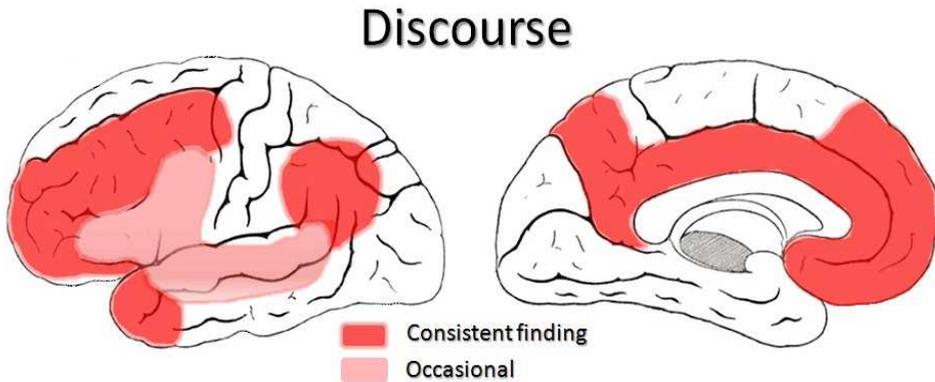
Fig. 4. Approximate locations of the system to process discourse

7. All together

Recent developments in brain imaging techniques include brain *tractography* with MRI, which has been promptly used to study human language. Brain tactography can be achieved through *diffusion tensor* and *diffusion spectrum* techniques. The main difference between the two of them depends on the deterministic vs. probabilistic approaches used to analyze the movement of water molecules within the main tracts substantiating cortico-cortical connections (de Schotten et al., 2011). It must be noted here, however, that the novelty and the relative scarcity of studies approaching language with this technique may explain certain inconsistencies between studies (for an extensive review, see Friederici, 2009).

Although it is well known after Karl Wernicke, the relevance for human language of the *arquate fasciculus* (AF) connecting Broca's and Wernicke's areas appears largely strengthened by tractographic techniques. The data also stress the relevance for language processing of other fascicles connecting anterior and posterior brain areas. A detailed description of all these connections is also emerging.

One of the first studies applying tractography to approach language was developed by Catani et al. (2005). These authors reported a direct strong connection between Broca's and Wernicke's areas through the FA, but given the fact that the areas actually connected covered a wider territory than the classical Broca's and Wernicke's areas (though, as shown earlier, the precise limits for these two areas may vary depending on the author), Catani and colleagues suggested to call them Broca's and Wernicke's *territories*, respectively. Their results also revealed the existence of two additional but indirect pathways connecting Broca's and Wernicke's territories. One would run laterally, consisting of an anterior segment connecting Broca's territory and the inferior parietal cortex. The other would be a posterior segment connecting the inferior parietal cortex with Wernicke's territory. Given the apparent relevance of these two indirect segments, and the fact that the inferior parietal cortex appears the main meeting point for these indirect connections, Catani et al. (2005) suggested to call this region the *Geschwind's territory*, in the memory of Norman Geschwind, who already proposed a relevant role of the inferior parietal cortex in language. This region largely overlaps with semantic areas involved in word and discourse processing, as we have seen.

The AF seems to have evolved substantially in the human brain from tiny tracts connecting the IFG with the posterior part of BA 22 and the inferior parietal regions, already present in the macaque brain. These connections appear more robust and abundant in the chimpanzee, thereafter reaching the plainest robustness of the human brain (Rilling et al., 2008). Actually, one of the main differences between the human and the chimpanzee brains in this regard is the notable expansion of the posterior ramifications of the AF, which spread not only to involve Wernicke's area and surrounding parietal regions, but also posterior portions of the MTG. The development of these connections, occurring particularly and noticeably within the left hemisphere, seem to have played a critical role in the evolution of human language.

Interestingly, two other tracts connecting anterior and posterior regions seem relevant in language processing. One is the superior longitudinal fasciculus (SLF), connecting Broca's area (particularly, BA 44) with the posterior temporal lobe, namely in the STG and the MTG and also involving portions of BA 40. As this tract runs parallel to the AF, several authors (e.g., Rilling et al., 2008) consider both as representing together a functional unit called the *dorsal stream*. The other connection is more primitive; part of it is actually the most developed fronto-temporal connection in the macaque brain and conveys the ventral portion of the extreme capsule and the uncinate fasciculus. Through these connections, the IFG is connected with the anterior and posterior STG (Frey et al., 2008; Rilling et al., 2008), and it is indeed possible that at least part of this *ventral stream* is preferentially used in simpler grammar such as finite-state, relatively accessible to other non-human primates (Friederici et al., 2006).

Finally, there are evidences for an additional number of connections importantly involved in language, most of them located locally within the IFG and the STG (Friederici, 2009).

8. Conclusions

The moment arrives to summarize and interpret the major milestones that could be elucidated from the preceding exposition. In the following, we will also express a number of reflections on human language using brain function as a main perspective.

A first and relatively robust conclusion that can be extracted so far is that the human brain contains at least two major "centers of gravity", or main hubs in the networks devoted to language processing. These foci are, on the one hand, the left inferior frontal gyrus (IFG) and, on the other, the left superior temporal gyrus (STG), the latter probably spreading to the superior temporal sulcus (STS) and posterior portions of the middle temporal gyrus (MTG) as well as to some parts of the inferior parietal cortex. Both foci are highly and densely interconnected by means of several tracts, the most outstanding one being the arquate fasciculus (AF). Most of the primary functions and processes involving these foci are seemingly phonological/articulatory and syntactic in nature. These two main hubs are located in perisylvian areas and appear critical for human language. Actually, the main loci of the cerebral lesions yielding core symptoms highly specific of language are the perisylvian areas; the most conspicuous aphasias are usually the consequence of lesions affecting either these regions or the AF (e.g., LaPointe, 2011).

If the depiction in the preceding paragraph can be taken as relatively robust, the same is not the case when we attempt to subdivide each hub (IFG and STG). An approximate

depiction seems that as we move from more posterior/dorsal regions to more anterior/ventral in the left IFG, a gradient of activations can be found to be specifically involved (in this order) in phonology/articulation, syntax, and semantics. A similar gradient could be found in the STG when moving from the primary auditory association areas in or around Hesch's gyrus, spreading widely to both anterior and posterior regions in the STG, probably covering also parts of the inferior parietal cortex. In the latter case, the gradient seems to cover, following this order, phonology/articulation and syntax. If we want to expand these functions to semantic processes, then STS and at least several portions of the MTG should be included.

From there, the system spreads to notably many other brain regions, comprising, posteriorly, large portions of the whole temporal lobes, including the temporal poles and part of the basal regions, as well as significant portions of the parietal cortex. Frontally, the system spreads to more anterior regions, including large extensions of the prefrontal cortex; among them, an area showing the most substantial increase in size in humans when compared to other primates and importantly involved in general intelligence. Significant medial regions, both in the prefrontal cortex and in the parietal cortex, are also included in this system. This *extended language network* (using an expression coined by Ferstl et al., 2008) largely overlaps with the *human default system*, a bilateral network in the human brain active when we are involved in "internal" mental tasks. If the linguistic message implies the visualization or representation of a given situation, then the corresponding primary or secondary areas of the neocortex can be activated, either motor or perceptual.

The system can therefore be viewed as a continuous flux of information spreading from perisylvian areas toward multiple, distant areas. In turn, it also seems that the limits between linguistic and non-linguistic processes within this system appear blurred. An overall rule seems to be that the closer we move toward the sylvian fissure, the more specifically linguistic the process is. But even in this case (as we have seen), these regions are not exclusively linguistic.

Finally, that the flux of information spreads from perisylvian areas toward extensive regions of the cerebral cortex (actually, nearly all portions of the cortex appear susceptible of being involved) does not necessarily mean that this spreading strictly follows a temporal (sequential) order. Actually, brain networks continuously fire at different frequencies (e.g., Buzsáki, 2006), and it is plausible that information fluxes continuously in a reciprocal way and almost simultaneously between perisilvian and more distant areas. This would be a possible underlying mechanism explaining the large number of mutual influences from one structural layer of language (phonology, syntax, and semantics) to each other, as reported in the literature (e.g., Pulvermüller et al., 2009b). Indeed, considering that there are about 10.000 connections per neuron in the cerebral cortex, firing up to 1.000 times per second and therefore performing a comparable number of calculations (Previc, 2009), a parallel or at least cascade mode of operation of the whole (extended) language network emerges as a very plausible picture. On the other hand, the centrality of auditory/verbal (i.e., phonological/articulatory) information in human language would be consistent with the position of the two main hubs involved in language processing and the direction of the information flux spreading from them as primary receptors of language information to widespread areas, even if the overall processes largely unfold in parallel.

9. Acknowledgements

10. References

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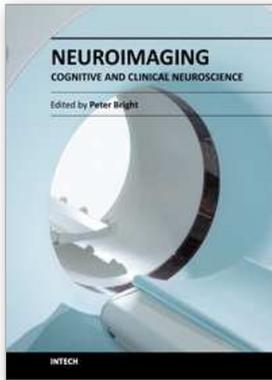
Neuroimaging - Cognitive and Clinical Neuroscience

Edited by Prof. Peter Bright

The rate of technological progress is encouraging increasingly sophisticated lines of enquiry in cognitive neuroscience and shows no sign of slowing down in the foreseeable future. Nevertheless, it is unlikely that even the strongest advocates of the cognitive neuroscience approach would maintain that advances in cognitive theory have kept in step with methods-based developments. There are several candidate reasons for the failure of neuroimaging studies to convincingly resolve many of the most important theoretical debates in the literature. For example, a significant proportion of published functional magnetic resonance imaging (fMRI) studies are not well grounded in cognitive theory, and this represents a step away from the traditional approach in experimental psychology of methodically and systematically building on (or chipping away at) existing theoretical models using tried and tested methods. Unless the experimental study design is set up within a clearly defined theoretical framework, any inferences that are drawn are unlikely to be accepted as anything other than speculative. A second, more fundamental issue is whether neuroimaging data alone can address how cognitive functions operate (far more interesting to the cognitive scientist than establishing the neuroanatomical coordinates of a given function - the where question).

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