

Review

Interaction between lexical and grammatical language systems in the brain

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Abstract

This review concentrates on two different language dimensions: lexical/semantic and grammatical. This distinction between a lexical/semantic system and a grammatical system is well known in linguistics, but in cognitive neurosciences it has been obscured by the assumption that there are several forms of language disturbances associated with focal brain damage and hence language includes a diversity of functions (phoneme discrimination, lexical memory, grammar, repetition, language initiation ability, etc.), each one associated with the activity of a specific brain area. The clinical observation of patients with cerebral pathology shows that there are indeed only two different forms of language disturbances (disturbances in the lexical/semantic system and disturbances in the grammatical system); these two language dimensions are supported by different brain areas (temporal and frontal) in the left hemisphere. Furthermore, these two aspects of the language are developed at different ages during child's language acquisition, and they probably appeared at different historical moments during human evolution. Mechanisms of learning are different for both language systems: whereas the lexical/semantic knowledge is based in a declarative memory, grammatical knowledge corresponds to a procedural type of memory. Recognizing these two language dimensions can be crucial in understanding language evolution and human cognition.

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1. Introduction

It is generally supposed that language presents a continuous progression in complexity, so during child language development, as throughout human history [16,30,69]. Thus, it is accepted that normally the child learns the first words about the age of 12 months [104]. Around this age the child acquires a new ability that he or she previously did not have: the ability to repeat. This ability to repeat correlates with the maturation of the arcuate fasciculus [109]. So-called Broca's area corresponds to the region of the left hemisphere involved in language production; it corresponds to the third frontal gyrus, located anterior to the face area of the motor cortex and above the Sylvian fissure. Damage in this area results in the language disturbance known as Broca aphasia. Wernicke's area is located in the posterior and superior part of the temporal lobe (first and second temporal gyri) of the left hemisphere, corresponding to the auditory association area of the left hemisphere. Damage in this area results in the language disturbance known as Wernicke aphasia. The arcuate fasciculus is the neural pathway connecting the posterior part of the temporoparietal junction (Wernicke's area) with the frontal cortex (Fig. 1).

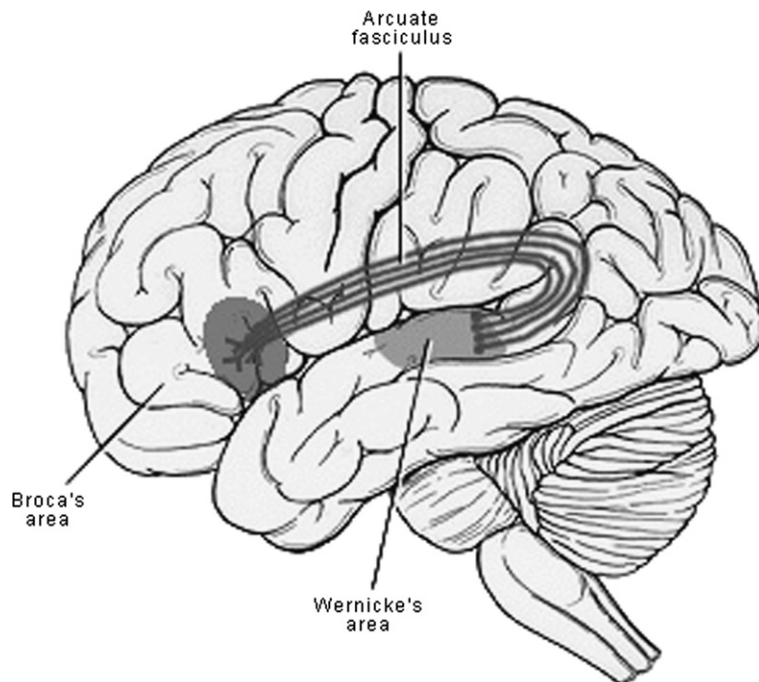


Fig. 1. Traditionally it has been accepted that there are two major areas involved in language: frontal Broca's area and temporal Wernicke's area. It has been assumed that the arcuate fasciculus connects these two cortical areas.

Table 1

Some names used to refer to the two fundamental aphasic syndromes. In the first one the disturbance is located at the lexical/semantic level, whereas in the second case, the disturbance corresponds to a grammatical impairment.

Receptive	Expressive
Sensory	Motor
Posterior	Anterior
Fluent	Non-fluent
Paradigmatic disorder	Syntagmatic disorder
Decoding disorder	Coding disorder
Wernicke-type	Broca-type

Sometime later, when the vocabulary reaches a large enough number of words, the child begins to combine them, initially two words, further three and more words, some of them with a purely connecting (grammatical) function [69]. Consequently, there is a steady progression in language evolution and language development.

In this review it is emphasized that human language includes two rather different dimensions: lexical/semantic (vocabulary) and grammatical (morphosyntax), which are correlated with two different evolutionary patterns. The lexical/semantic system (i.e., representing external elements with sounds) has its roots in animal communication systems, and most likely has existed since the early hominids, and possibly even before [10,11,93]. Here it is emphasized that the emergence of grammar (set of structural rules governing the composition of sentences – syntax and words – morphology) in human evolution was not just a quantitative but rather a qualitative change [38], probably associated with the emergence of the so-called *metacognitive executive functions* (problem solving, planning, concept formation, strategy development and implementation, controlling attention, working memory, and the like) [7]. The emergence of grammar represents indeed the most crucial leap in human language evolution. These two language systems (lexical/semantic and grammatical) are correlated with the activity of two distinct brain areas of the left hemisphere (temporal and frontal) (e.g., [22,160]). They are mediated by different learning processes (explicit and implicit memory) [39,40,89,107,146,147] and they appear during ontogeny and phylogeny at two different moments [69,30]. Clinical observations clearly demonstrate that there are two major aphasia syndromes (Wernicke-type and Broca-type aphasia) (for a review, see: [9]) due to damage in rather different brain areas and associated with the impairment of each one of these language dimensions (lexical/semantic in Wernicke aphasia and grammatical and Broca aphasia).

2. Clinical evidence

Since the initial reports about language disturbances associated with brain pathology, it has been evident that there are two basic aphasic syndromes, named in different ways (see Table 1), but roughly corresponding to Wernicke-type aphasia and Broca-type aphasia [1,2,17,19,45,53,63,64,77,80,87,111,127,138,159] (see [141] for review). *This is a most basic departure point in aphasia: Aphasia is not a single and unified clinical syndrome, but two rather different (even opposed) clinical syndromes.*

These two major aphasic syndromes have been related with the two basic linguistic operations: selecting (language as paradigm; that is, language as a lexical/semantic system) and sequencing (language as syntagm; that is, language as a grammatical system) [75,74,86]. Jakobson [72] proposed that aphasia tends to involve one of two types of linguistic deficiency. A patient may lose the ability to use language in two rather different ways: the language impairment can be situated on the paradigmatic axis (similarity disorder due to an impairment in the lexical/semantic knowledge) or the syntagmatic axis (contiguity disorder due to an impairment in the grammatical system).

Luria [86] emphasized that the selection disorder can be observed at different levels of the language, corresponding to different aphasia subtypes: phoneme selection (acoustic agnosic aphasia), word selection (acoustic amnesic aphasia), and meaning selection (amnesic aphasia). By the same token, the contiguity disorder can be observed at different levels: sequencing words (kinetic motor aphasia – Broca aphasia) or sequencing sentences (dynamic aphasia – transcortical motor aphasia). Noteworthy, different subtypes of Wernicke aphasia are frequently distinguished (e.g., [6]) and Luria's acoustic agnosic, acoustic amnesic, and amnesic aphasia can be considered as subtypes of the language impairment syndrome usually referred to as a whole as Wernicke aphasia.

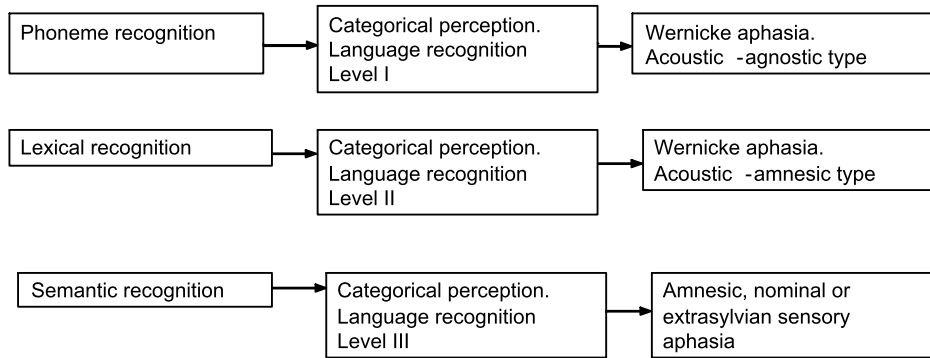


Fig. 2. Three different deficits underlie Wernicke-type aphasia: (a) phoneme recognition defects, (b) lexical recognition impairments, and (c) lexical/semantic association deficits, each one resulting in a specific Wernicke aphasia subtype (adapted from [5]).

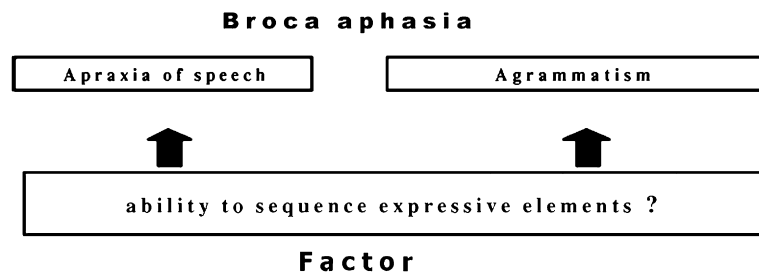


Fig. 3. The impairment of a single factor (ability to sequence expressive elements?) may account for the two major manifestation observed in cases of Broca aphasia (adapted from [12]).

2.1. Wernicke aphasia: grammar without content

The Wernicke-type of aphasia represents the clinical syndrome characterized by impairments in the lexical/semantic system. In Wernicke aphasia, the lexical repertoire tends to decrease and language understanding difficulties are evident. Wernicke aphasia patients do not fully discriminate the acoustic information contained in speech. Lexical (word) forms and semantic (meaning) associations become deficient. Patients have problems in recalling the words (memory of the words) and also in associating the words with specific meanings. It means at least three different deficits underlie Wernicke-type aphasia: (a) phoneme discrimination defects; (b) verbal memory defects; and finally (c) lexical/semantic association deficits [5,9] (Fig. 2).

In the Wernicke-type of aphasia obviously the language defect is situated at the level of the meaningful words (nouns). Phoneme and word selection are deficient, but language syntax (contiguity: sequencing elements) is well preserved and even overused (paragrammatism in Wernicke aphasia). Nouns seem to depend on an organized pattern of brain activity. Contemporary clinical and neuroimaging studies have corroborated that different semantic categories are differentially impaired in cases of brain pathology (e.g., [123]).

2.2. Broca aphasia: content without grammar

The Broca-type of aphasia represents the clinical syndrome characterized by impairments in the sequencing process (grammar). It is usually recognized that Broca aphasia has two different distinguishing characteristics: (a) a motor component (lack of fluency, disintegration of the speech kinetic melodies, verbal-articulatory defects, etc. that is usually referred to as apraxia of speech); and (b) agrammatism (e.g., [19,87,52,78]). If both defects are simultaneously observed (i.e., they are very highly correlated), it simply means they both are just two different manifestations of a single underlying defect. It is not easy to understand what could be the single factor responsible for these two clinical manifestations; but it may be a kind of “inability to sequence expressive elements” [9,12] (Fig. 3).

Broca's area, most likely, is not specialized in producing language, but in certain neural activities that can support not only skilled movements required for speech, but also morphosyntax. It is interesting to note that deaf-mute subjects

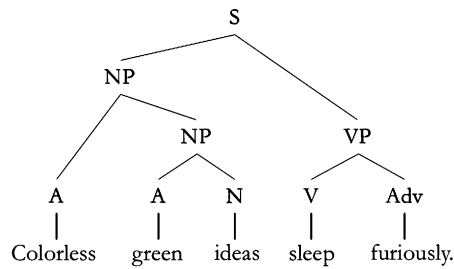


Fig. 4. The sentence (S) “Colorless green ideas sleep furiously” includes a nominal phrase (NP) and a verbal phrase (VP). The sentence is grammatically correct but semantically empty [26].

(who, in consequence, have never produced verbal articulatory movements) present a virtually total impossibility to learn, understand, and use language grammar [112]. Probably, the lack of normal verbal articulatory development and practice may contribute to this lack of normal grammatical development.

3. Linguistic evidence

This distinction between a lexical/semantic and a grammatical system is obviously well known in linguistics. For instance, Jakobson [73] stated that language includes two different language dimensions or axes (paradigmatic – i.e., lexical/semantic; and syntagmatic – i.e., grammatical). Chomsky [26,27] clearly illustrated that the lexical/semantic system is independent from the grammatical system; that is, a sentence can be grammatically correct but semantically empty. To illustrate this point, the original example used by Chomsky [26] can be used (Fig. 4).

Unfortunately, in cognitive neurosciences, such a distinction between a lexical/semantic system and a grammatical system is frequently obscured by the assumption that there are several (seven and even more) forms of language disturbances (aphasias) (e.g., [18,19,77,53,87,156]) associated with focal brain damage. There is the implicit assumption that language includes a diversity of functions (phoneme discrimination, lexical memory, grammar, repetition, language initiation ability, etc.), each one associated with the activity of a specific brain area. The different aphasia subtypes (Broca aphasia, conduction aphasia, Wernicke aphasia, aphasia of the supplementary motor area, transcortical sensory aphasia, etc.) are interpreted as conceptually equivalent, and in each one a specific language function or ability is supposed to be disturbed. Hence, there are seven (and even more) language functions.

4. Learning evidence

Two major memory systems are frequently distinguished in contemporary memory literature: declarative memory (divided into semantic and episodic or experiential) and procedural memory [144] (see Fig. 5). It has been suggested that the lexical/semantic and grammar aspects of the language are subserved by different neuroanatomic brain circuitries and depend upon these two different memory systems [39,40,107,146,147]. Whereas lexical/semantic aspects of the language depend on a declarative semantic memory (knowledge about the meaning of the words), grammar depends on a procedural memory.

Some studies have demonstrated the role of the basal ganglia in grammar learning and use. Recent research has supported that striatal-damaged patients are impaired with conjugation rules while retaining lexical knowledge of irregular verbs [139,141,148]. Teichmann et al. [140] found that patients with Huntington’s disease are selectively impaired for rule application but lexical abilities are spared. The authors assume that the striatum has a core function in linguistic rule application generalizing to perceptive aspects of morphological operations and pertaining to implicit language processes. In addition, they suggest that the striatum may enclose computational circuits that underpin explicit manipulation of regularities. Macoir et al. [89] report a case of a mild aphasic patient who showed procedural deficits in the presence of preserved declarative memory abilities. Several experiments to explore rule application in morphology, syntax and number processing were administered. Results at least partly supported the differentiation between declarative and procedural memory.

Studies investigating artificial grammar systems have shown similar results. Thus, it has been observed that the posterior part of the inferior frontal gyrus (BA44) and the ventral premotor cortex (BA6) seem to play a fundamental role in grammar processing [46,105]. Opitz and Kotz [106] tested patients with ventral premotor cortex lesions in an arti-

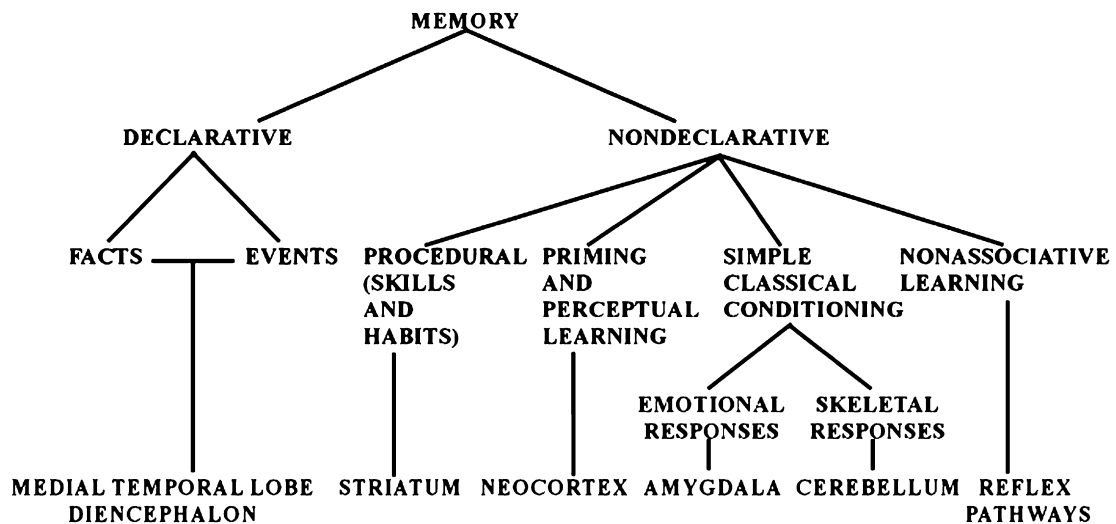


Fig. 5. Two different languages systems are currently distinguished: declarative and nondeclarative. Procedural memory is indeed a particular type of nondeclarative memory. Whereas lexical/semantic knowledge represents a type of declarative memory mediated by the medial temporal lobe, grammar has been related with procedural memory, depending upon the striatum (part of the basal ganglia of the brain including the caudate nucleus and the lentiform nucleus) (adapted from [131]).

ficial grammar learning task. Compared to matched controls, patients displayed impaired acquisition of the artificial grammar, supporting the assumption that these motor-related areas play a crucial role in grammar learning and use.

Friederici et al. [47] analyzed the neurophysiological preconditions of syntax acquisition. They state that early language learning seems to be based on the bilateral temporal cortices. However, subsequent syntax acquisition apparently primarily recruits a neural network involving the left motor related frontal cortex and the temporal cortex connected by a ventrally located fiber system. The late developing ability to comprehend syntactically complex sentences appears to require a neural network that connects Broca's area to the left posterior temporal cortex via a dorsally located fiber pathway.

Lexical/semantic aspects of the language are explicitly learned and represent a type of knowledge we are aware of (declarative memory). It depends on retro-rolandic cortical structures and the hippocampus. Grammar (language sequences, contiguity) on the other hand, is acquired incidentally. Procedural memory for grammar supposes implicit language knowledge. Procedural grammatical learning is related to the execution of sequences of elements (skilled articulatory acts and grammar) used for speaking but also for syntax. Procedural memory is related with frontal/subcortical circuitries [145].

Broca's area damage results in a defect in grammar and also in an inability to find verbs [13,32]. In consequence, brain representation of actions (verbs) and brain representation of grammar are coincidental. Using verbs and using grammar depends upon the very same type of brain activity and both are simultaneously disrupted in cases of Broca aphasia. It can be conjectured that verbs and grammar appeared simultaneously in human language evolution; or rather, they are the two sides of the same coin. Furthermore, grammar is associated with oral praxis skills (i.e., agrammatism and apraxia of speech are observed simultaneously in Broca aphasia), and hence, all three have appeared simultaneously in the evolution of human language: using verbs, using grammar, and rapidly sequencing movements with the articulatory organs. It can be speculated that grammar, speech praxis movements, and using verbs appeared roughly simultaneously in human history. Therefore, they are strongly interrelated and depend upon a common neural activity.

5. Anatomical evidence

5.1. The lexical/semantic system

Paleoneurology (study and analysis of fossil endocasts) can significantly contribute to the understanding of the origins of the contemporary human language. Paleoneurology can shed light in understanding the evolution of those brain areas involved in language processing.

It is known that in monkeys, the temporal lobes are involved in recognizing the sounds and calls of the own species [115,116,136,155,157] and evidently, the temporal lobe was a crucial area in developing a complex lexical/semantic system. Human sounds and calls are obviously at the origin of language words. Gannon et al. [48] observed that the anatomic pattern and left hemisphere size predominance of the planum temporale, a language area of the human brain, are also present in chimpanzees. They found that the left planum temporale was significantly larger in 94% of chimpanzee brains examined. Hence, the crucial lexical/semantic difference between humans and chimpanzees cannot be related to the planum temporale. By the same token, it has been observed that anatomical temporal-lobe asymmetries favoring the left hemisphere are found in several Old and New World monkey species [66]. Hopkins and Nir [71] examined whether chimpanzees show asymmetries in the planum temporale for grey matter volume and surface area in a sample of 103 chimpanzees from magnetic resonance images. The results indicated that, overall, the chimpanzees showed population-level leftward asymmetries for both surface area and grey matter volumes. Furthermore, chimpanzees that prefer to gesture with their right hand had significantly greater leftward grey matter asymmetries compared to ambiguously- and left-handed apes. Development of a human lexical/semantic communication system in consequence cannot be related to the temporal lobe asymmetry because this asymmetry is observed long before the beginning of the human language. This asymmetry seems to be related with a left temporal lobe specialization for intra-specific communication system. Spocter et al. [130] affirm that leftward asymmetry of Wernicke's area originated prior to the appearance of modern human language and before our divergence from the last common ancestor.

Nonetheless, differences between humans and nonhuman primates can be related with the temporal lobe volume. Rilling et al. [117] analyzed the volume of the temporal lobe in different primates. Whole brain, T1-weighted MRI scans were collected from 44 living anthropoid primates spanning 11 species. The surface areas of both the entire temporal lobe and the superior temporal gyrus were measured, as was temporal cortical gyrification (complexity and number of gyri). Allometric regressions of temporal lobe structures on brain volume consistently showed apes and monkeys to scale along different trajectories, with the monkeys typically lying at a higher elevation than the apes. Within the temporal lobe, overall volume, surface area, and white matter volume were significantly larger in humans than predicted by the ape regression lines. The largest departure from allometry in humans was for the temporal lobe white matter volume which, in addition to being significantly larger than predicted for brain size, was also significantly larger than predicted for temporal lobe volume. Among the nonhuman primate sample, *Cebus* have small temporal lobes for their brain size, and *Macaca* and *Papio* have large superior temporal gyri for their brain size. The observed departures from allometry might reflect neurobiological adaptations supporting species-specific communication in both humans and Old World monkeys. The authors concluded that the entire human temporal lobe and some of its component structures are significantly larger than predicted for a primate brain of human size. The most dramatic allometric departure is in the volume of the human temporal lobe white matter, which, in addition to being large relative to brain size, is also large relative to temporal lobe size. These allometric departures in humans could reflect a reorganization of the temporal lobes driven by expansion of the language cortex and its associated connections. It is interesting to note that in primates the superior temporal gyrus contains neurons tuned to species-specific calls, the magnitude of different species' relate to the repertoire of vocal communicative signals as reflections of the complexity of their respective social environments.

It has been calculated that this enlargement of the temporal lobe may have occurred some 200–300 thousand years ago [79]. It can thus be conjectured that hominids existing before the contemporary *Homo sapiens sapiens* could have developed certain complex lexical/semantic communication systems. For instance, it could be speculated that Neanderthal man (*Homo sapiens neanderthalensis*) could have had a relatively complex language at least as a lexical/semantic system.

5.2. Understanding Broca's area

In the last decade there has been a significant interest in re-analyzing the function of Broca's area (e.g., [56,58,143]). So-called Broca's area includes the pars opercularis (Brodmann's area-BA44) and probably the pars triangularis (BA45) of the inferior frontal gyrus [44]. BA45 probably is more "cognitive" than BA44, which seems to be more motor and more phonetic. From the traditional point of view, Broca's area corresponds to BA44, but several contemporary authors also include BA45. In the traditional aphasia literature it was assumed that damage in Broca's area was responsible for the clinical manifestations observed in Broca's aphasia. Only with the introduction of the CT scan

did it become evident that the damage restricted to Broca's area was not enough to produce the "classical" Broca's aphasia; extension to the insula, lower motor cortex, and subjacent subcortical and periventricular white matter is also required [3]. "Broca's area aphasia" ("minor Broca's aphasia") is characterized by mildly non-fluent speech, relatively short sentences and mild agrammatism; phonetic deviations and a few phonological paraphasias can be observed [99]; some foreign accent can also be noticed [15]. Interestingly, electrical stimulation of Broca's area enhances implicit learning of an artificial grammar [35].

Simultaneously including both BA44 and BA45 in Broca's area is problematic. BA44 is a premotor dysgranular area, whereas BA45 has a granular layer IV and belongs to the heteromodal prefrontal lobe (granular cortex) [94]. So, from a cytoarchitectonic point of view, BA44 and BA45 are quite different. BA44 is a premotor area whereas BA45 corresponds to the prefrontal cortex. From the aphasia perspective, some authors have referred to different clinical manifestations associated with damage in BA44 (Broca-type aphasia) and BA45 (transcortical motor/dynamic aphasia) (e.g., [87]). Broca's area is, more than likely, involved in different language and language related functions [42]. Some authors have pointed out that indeed Broca's area is a collective term that can be fractionated in different sub-areas [84]. Hagoort [58,59] refers to the "Broca's complex", including BA44 (premotor), and also BA45 and BA47 (prefrontal cortex). He argues that Broca's complex is not a language-specific area, and it becomes active during some nonlanguage activities, such as mental imagery of grasping movements [34]. Functional defined sub-regions could be distinguished in Broca's complex: BA47 and BA45 are involved in semantic processing, BA44, BA45, and BA46 participate in syntactic processing, and BA44 is involved in phonological processing [67,124]. Hagoort [58] proposes that "the common denominator of Broca's complex is its role in selection and unification operations by which individual pieces of lexical information are bound together into representational structures spanning multiword utterances" (p. 166). Its core function is, consequently, binding the elements of the language.

Thompson-Schill [143] analyzed the different deficits observed in cases of damage in Broca's area: articulation, syntax, selection, and verbal working memory, suggesting that there may be more than a single function of Broca's area. The author proposes a framework for describing the deficits observed in different patients. He suggested that Broca's area may be involved in selecting information among competing sources. Fadiga, Craighero, and Roy [41] speculate that the original role played by Broca's area relates to generating/extracting action meanings; specifically, organizing/interpreting the sequence of individual meaningless movements. Ardila and Bernal [12] conjectured that the central role of Broca's area was related to sequencing motor/expressive elements. Novick, Trueswell, and Thompson [102] consider that the role of Broca's area is related with a general cognitive control mechanism for the syntactic processing of sentences.

Grodzinsky [54,55] presented an extensive analysis of the role of Broca's area. He proposed that most syntax is not located in Broca's area and its vicinity (operculum, insula, and subjacent white matter). This brain area does have a role in syntactic processing, but a highly specific one: it is the neural home to receptive mechanisms involved in the computation of the relation between transformationally moved phrasal constituents and their extraction sites (syntactic movement). He further assumes that Broca's area is also involved in the construction of higher parts of the syntactic tree in speech production. Interestingly, blood flow in Broca's area increases when participants process complex syntax [24]. Santi and Grodzinsky [125] also recognize its role in working memory related with a specific syntactic role in processing filler-gaps dependency relations. Syntax is indeed neurologically segregated, and its components are housed in several distinct cerebral locations, far beyond the traditional ones (Broca's and Wernicke's regions). A new brain map for syntax would also include portions of the right cerebral hemisphere [57].

Haverkort [61] emphasizes that a clear distinction should be established between linguistic knowledge and linguistic use. Patients with Broca's aphasia have a limitation in the use of grammar, but their grammatical knowledge is available. Broca's aphasia patients present a simplified syntax and phrases are short. They select simpler syntactic structures that are less complex because they impose less of a burden on working memory. In consequence, one major factor in Broca's aphasia relates to an impairment in verbal working memory.

Interestingly, electrical stimulation of Broca's area enhances implicit learning of an artificial grammar. De Vries et al. [35] selected 30 healthy subjects to participate in a real or sham stimulation over Broca's area during the acquisition of an artificial grammar. Performance during the acquisition phase was comparable between groups. In a later task of detecting syntactic violations, performance improved significantly after the real stimulation resulting in an overall better performance. A second experiment where some subjects received real stimulation over an area unrelated to artificial grammar learning further supported the specificity of these effects to Broca's area. The authors concluded that Broca's area is specifically involved in rule-based knowledge, and hence, in the ability to detect syntactic violations.

In summary, regardless that expressive language disturbances have been associated for over a century with damage in the left inferior frontal gyrus (later known as “Broca’s area”), currently there is incomplete agreement about its limits and its specific functions in language. Different proposals have been presented to explain language disturbances in so-called Broca’s aphasia, including: binding the elements of the language [58]; selecting information among competing sources [142]; generating/extracting action meanings [41]; sequencing motor/expressive elements [12]; cognitive control mechanism for the syntactic processing of sentences [102]; construction of higher parts of the syntactic tree in speech production [54,55]; and verbal working memory [61].

5.3. *Brain organization of nouns and verbs*

It has been observed that verbs and nouns clearly depend on the activity of different brain areas, and naming objects and actions are disrupted in cases of different types of brain pathology. Speaking or thinking in nouns increased activity in the left temporal lobe, whereas speaking or thinking in verbs activated the Broca frontal area [114]. By the same token, impairments in finding nouns are associated with temporal lobe pathology, whereas impairments in finding verbs is associated with left frontal damage and Broca aphasia [13,32]. It has been reported that the damage restricted to Broca’s area can result in a selective defect in finding verbs and name actions whereas objects, colors, body parts, and qualities can be named in a normal way [13]. It has also been observed that naming actions activates the left frontal operculum roughly corresponding to Broca’s area [33].

Interestingly, when using verbs, not only Broca’s area is activated, but also some additional brain areas, according to the specific meaning of the verb. Thus, Yang et al. [161] studied the dissociation and association of the embodied representation of tool-use verbs and hand verbs using fMRI. All verb conditions showed common activations in areas of left middle frontal gyrus, left inferior frontal gyrus (BA44/45) and left inferior parietal lobule relative to rest, and all conditions showed significant effects in premotor areas within the mask of hand motion effects. Contrasts between tool-use verbs and hand verbs demonstrated that tool verbs elicited stronger activity in left superior parietal lobule, left middle frontal gyrus and left posterior middle temporal gyrus.

Brain organization of the lexical/semantic system seems to be related to the type of association between words and perceptions (percepts, meanings). When the words are associated with one’s own body information (e.g., the word “finger”), brain representation of the lexicon seems associated with a parietal extension; when the word has visual associations (e.g., the word “book”), an occipital extension is found [123]. That is, the temporal lobe plays the role of discriminating the speech sounds and sequences of sounds (lexicon) but the meaning (semantic) requires an association with one or several sensory modalities.

In anomia it has been traditionally recognized that naming body parts, external objects and colors depend (and are altered) upon the activity of different brain areas [65]. It has also been found that finer distinctions can be made with regards to naming defects, which can be limited to a rather specific semantic category (e.g., people’s names, living things, tools, geographical names, etc.) (e.g., [60,51,88,158]) and even as specific as “medical terms” [31]. A brain “mapping” of the memory organization of different semantic categories could be supposed.

That means that the neural correlates of naming concrete entities such as tools (with nouns) and naming actions (with verbs) are partially distinct: the former are linked to the left inferotemporal region, whereas the latter are linked to the left frontal opercular and left posterior middle temporal regions [144]. Simply speaking, nouns and verbs are related with different brain systems.

6. **Developmental evidence**

What was the crucial leap for the development of language grammar? (i.e., syntagmatic dimension of the language). Obviously grammar was initially simple, and “sentences” contained only two words. How did one link two words to create a new higher-level unit (syntagm)? Further, how did one mark the relationship between the two words? The mechanism has to be the simplest one, and it is not unlikely that it may be similar to the mechanism observed in children during language development.

Suppose that we have two lexical units:

animal – fruit

Different relations between these two words can exist; but the relationship requires an action (verb); it means that there is an interaction between both elements, such as: animal *eats* fruit; animal *has* fruit, animal *receives* fruit; animal *likes* fruit, etc.

In consequence, before creating a syntagmatic relationship between the words, different word categories have to be separated (e.g., objects and actions).

For creating a phrase, indeed only two types of elements are really required: nouns (nominal phrase) and verbs (verbal phrase). If putting together two words corresponding to two different classes (e.g., animal sleep), there is already a syntagm and grammar has appeared. In childhood language it is observed that words corresponding to two different classes are combined such as, “big dog,” “food good,” “dad gone.” They contain a grammar, because the words belong to two different classes. In the first two examples (“big dog,” “food good,”), there is an existence verb (to be) that is implicit and omitted (as currently observed in some contemporary languages, such as Russian). “Mom dad” is not a phrase, but “mom big” is a primitive sentence.

Brown [23] found that the majority of the utterances at the beginning of the child’s grammar could be described by a small set of functional relationships between words:

- (1) “agent + action” (baby kiss)
- (2) “action + object” (pull car)
- (3) “agent + object” (daddy ball)
- (4) “action + location” (sit chair)
- (5) “object + location” (cup table)
- (6) “possessor + possession” (mommy sock)
- (7) “object + attribute” (car red)
- (8) “demonstrative + object” (there car)

The crucial point in emerging grammar is not the extension of the vocabulary. What is really crucial is to have words corresponding to two different classes that can be combined to form a higher-level unit (syntagm). One of the words has to be a noun; the other is a verb. Hence, the problem becomes: how verbs appeared. To create nouns does not seem so complicated (e.g., nouns can be created departing from onomatopoeias, etc. [162]). Verbs, on the other hand, can be created departing from the nouns, but with the meaning of an action (e.g., baby kiss). Action usually means moving, doing, executing, not simply perceiving and associating with some visual (or auditory or tactile) information. “Kiss” can be associated with some sensory information, and obviously the temporal, parietal, and occipital brain areas have to participate (“kiss” as a noun). “Kiss” can also be associated with an action, and obviously the frontal areas have to be involved in this second type of association (“kiss” as a verb). It is well known that impairments in finding nouns are associated with temporal lobe pathology, whereas impairments in finding verbs are associated with left frontal damage and Broca’s aphasia [13,32].

Grammatical words, such as prepositions, have an original spatial meaning. Prepositions link words (nouns, pronouns and phrases) in a sentence. A preposition usually indicates the temporal, spatial or logical relationship of its object to the rest of the sentence (e.g., the pencil is **on** the table; I go **to** class; etc.). That is, a preposition locates the noun in space (or in time). Simply speaking, the use of preposition as a basic grammatical element supposes a representation of actions (moving, doing, executing).

7. Understanding language evolution

The origin of human language remains controversial and different explanatory proposals have been presented (e.g., [11,21,30,103,132]). Ardila [8] suggested that human language evolved through three different stages:

- (1) Initial communication systems using sounds and other types of information – such as gestures, etc., similar to the communication systems observed in other animals, including nonhuman primates [110].
- (2) Primitive language systems using combined sounds (words) but without a grammar (language as a lexical/semantic system). This type of language probably existed in other hominids [93] and could be linked to the holophrastic period in language development, observed in children around 1 to 1.5 years of age [69,104].

- (3) By the end of the second year, children begin to combine words into simple sentences. Initially, sentences have a telegraphic style (telegraphic speech) (around 24–30 months of age), including two-word utterances in which connecting elements are omitted (e.g., “dog big”) [69]; later, words with a grammatical function are found. Probably this type of language is historically recent and can be observed only in the *Homo sapiens* likely linked to some specific genetic mutations [38,149,150]. No question, the emergence of a grammatical language represents a crucial leap in human evolution.

It simply means that language likely initially emerges as a system of words with a particular content (meaning) (lexical/semantic system), and only later as a system of relations (grammatical system). Bickerton [20] developed the idea that a protolanguage must have preceded the full-fledged syntax of today’s discourse. Echoes of this protolanguage can be seen, he argued, (a) in pidgin languages, (b) in the first words of infants, (c) in the symbols used by trained chimpanzees, and (d) in the syntax free utterances of children who do not learn to speak at the normal age. Bickerton [20] considers that such a protolanguage existed already in the earliest *Homo* (about 2.3 to 2.4 million years), and was developed due to the pressure of the behavioral adaptations faced by *Homo habilis* (2.3 to 1.4 million years ago). Steels [132] argued that cultural evolution is a much more powerful process than usually assumed, and human language evolution has to rely less on genetic evolution.

7.1. Initial communication systems

It is easy to assume that at the beginning of the human language, communication systems were similar to the communication systems found in nonhuman primates. It is known that chimpanzees and other nonhuman primates in their natural environment can use some communication strategies [110]. Chimpanzees employ a variety of gestures and facial expressions to communicate and keep in touch with each other. They possess a simple repertoire of noises and postures (body language) that can be used in different contexts with specific communication purposes. Observations have been collected in different environments, including natural environments and captive groups in human controlled environments [91]. Chimpanzees make use of simple gestures, make facial expressions and produce a limited amount of vocalizations. Unlike humans, chimps only produce about 12 different vocalizations. In captive conditions and under human training, chimpanzees can learn some artificial languages and close to about 200 “words” [25,91].

7.2. Lexical/semantic communication systems

Different attempts have been made to teach nonhuman primates to use more complex communication systems. Initially, Hayes and Hayes [62] trained the chimp Vicki. She became able to produce only four different words in six years! (“mom,” “pa,” “cup,” and “up”). Other chimps and gorillas have also participated in communication training programs: Nim and Koko used signs; Sara used plastic chips; Lana, Sherman, and Austion manipulated combinations of buttons to communicate [50,83,108].

Regardless of the relatively large amount of meaningful elements that chimpanzees can learn, they fail in developing sequencing of elements (syntax).

Kanzi learned to use around 200 symbols on a portable electronic symbol board but learning grammar was not evident. It has been pointed out that while chimpanzees can learn to order their symbols to get what they want, it is not clear that they have mastered syntax [97,126]. The reason is that when they initiate communication, they often abandon the order they have learned and word order becomes random.

The question becomes: how did this type of simple communication system found in nonhuman primates in natural conditions (i.e., to use some few vocalizations, gestures and facial expressions) further developed into contemporary human language? Certain mechanisms potentially could be used to create meaningful sequences of sounds (i.e., words); for example, new words can be created departing from onomatopoeias, emotional expressions, interjections, gestures, etc. Indeed, a diversity of mechanisms has been proposed to account for how human words emerged [162]. This is an ability that is not found in nonhuman primates. Using these strategies certainly requires a brain notoriously more advanced than the chimpanzee’s brain. Interestingly, it has been found that the arcuate fasciculus is much smaller or absent in nonhuman primates (chimpanzees and macaques) compared with humans [118], potentially limiting the language repetition ability and the possibility to transmit language from parents to children.

7.3. Grammatical communication systems

So-called executive functions represent one of the most intensively studied neuroscience questions during the last decade (e.g., [49,95,134,135]). Disagreement persists, however, around the potential unitary factor in executive functions [98,133]. Ardila (2008) [7] emphasized that “action representation” (i.e., internally representing movements or actions) may constitute at least one basic executive function factor. It could be speculated that “action representation” and also “time perception” (potentially derived from action representation) may depend upon one single core ability (“sequencing?”).

Two departing observations are important to support the involvement of prefrontal cortex in motor representation:

1. Anatomical observation. Prefrontal cortex represents an extension and further evolution of the frontal motor areas [96,119]. It may be conjectured that the prefrontal lobe should participate in complex and elaborated motor (“executive”) activities.
2. Clinical observation. A diversity of motor control disturbances are observed in prefrontal pathology, such as perseveration, utilization behavior, paratonia, primitive reflexes, etc. (e.g., [14,151]).

Throughout recent history several authors have argued that thought, reasoning, and other forms of complex cognition (“metacognition”) depend on an internalization of actions. Vygotsky [152–154], for instance, proposed that thought (and in general, complex cognitive processes) is associated with some “inner speech”. Vygotsky represents the most classical author suggesting this interpretation for complex cognition. More recently, Lieberman [81,82] suggested that language in particular and cognition in general arise from complex sequences of motor activities.

The central point in Vygotsky’s [153] idea is that higher forms of cognition (“cognitive executive functions”) depend on certain mediation (language, writing or any other); the instruments used for mediating these complex cognitive processes are culturally developed. According to Vygotsky [152], the invention (or discovery) of these instruments will result in a new type of evolution (cultural evolution), not requiring any further biological changes. Thinking is interpreted as a covert motor activity (“inner speech”). Vocalization becomes unnecessary because the child “thinks” the words instead of pronouncing them. Inner speech is for oneself, while external, social speech is for others. In brief, Vygotsky [153] argued that complex psychological processes (metacognitive executive functions) derive from language internalization. Thinking relies on the development of an instrument (language or any other) that represents a cultural product.

Lieberman [81,82] refers specifically to the origins of language. He postulates that neural circuits linking activity in anatomically segregated populations of neurons in subcortical structures and the neocortex throughout the human brain regulate complex behaviors such as walking, talking, and comprehending the meaning of sentences. The neural substrate that regulates motor control (basal ganglia, cerebellum, and frontal cortex) in the common ancestor of apes and humans most likely was modified to enhance cognitive and linguistic ability. The cerebellum and prefrontal cortex are also involved in learning motor acts (e.g., [90,68]). Lieberman [81,82] proposes that the frontal regions of the cortex are implicated in virtually all cognitive acts and the acquisition of cognitive criteria; posterior cortical regions are clearly active elements of the brain’s dictionary. Real-word knowledge appears to reflect stored conceptual knowledge in regions of the brain traditionally associated with visual perception and motor control. Some aspects of human linguistic ability, such as the basic conceptual structure of words and simple syntax, are phylogenetically primitive and most likely were present in the earliest hominids. Lieberman [81,82] further suggests that speech production, complex syntax, and a large vocabulary developed in the course of hominid evolution, and *Homo erectus* most likely talked, had large vocabularies, and commanded fairly complex syntax.

These two authors (Vygotsky and Lieberman), although using rather different approaches, have both postulated that the development of language and complex cognition are related with some motor programs, sequencing, internalizing actions, and the like. Many other authors have presented a similar point of view (e.g. [70,76,85,100,113,129]). Some contemporary research seems to support this interpretation; for instance, Clerget, Winderickx, Fadiga, and Olivier [28] using transcranial magnetic stimulation to interfere transiently with the function of left BA44 in healthy individuals found that a virtual lesion of left BA44 impairs individual performance only for biological actions, and more specifically for object-oriented syntactic actions. The authors concluded that these findings provide evidence that Broca’s area plays a crucial role in encoding complex human movements, a process which may be crucial for understanding and/or programming actions.

The recent discovery of mirror neurons [37,121,122] could significantly contribute to the understanding of the brain organization for verbs. A mirror neuron is a neuron which fires both when an animal performs an action and also when the animal observes the same action performed by another animal. Mirror neurons were initially observed in monkeys [37], but in humans, brain activity consistent with mirror neurons has been found in the premotor cortex and the inferior parietal cortex [122,121]. These neurons (mirror neurons) appear to represent a system that matches observed events to similar, internally generated actions.

Transcranial magnetic stimulation and positron emission tomography (PET) experiments suggest that a mirror system for gesture recognition indeed exists in humans and includes Broca's area [120]. The discovery of mirror neurons in Broca's area might have important consequences for understanding brain language organization and language evolution [4,29]. An obvious implication of mirror neurons is that they can participate in the internal representation of actions, and the internal representation of actions may represent the origin of grammar. Neuroimaging data have showed that interactions involving Broca's area and other cortical areas are weakest when listening to spoken language accompanied by meaningful speech-associated gestures (hence, reducing semantic ambiguity), and strongest when spoken language is accompanied by self grooming hand movements or by no hand movements at all, suggesting that Broca's area may be involved in action recognition [128]. PET studies have associated the neural correlates of inner speech with activity of Broca's area [92]. De Zubicaray et al. [36] have emphasized the importance of Broca's area to covert verbalization.

In brief, there is some converging evidence that something like "action representation" may constitute the departing point for both, grammar and executive functions.

8. Conclusions

Regardless that the distinction between language as a lexical/semantic system and language as a grammatical system is evident in linguistics, this distinction has not been incorporated in contemporary cognitive neurosciences yet, probably due to the frequent assumption that there are several aphasia subtypes and thence, several language functions supported by diverse brain language subsystems. This assumption overlooks the most important and basic departing point in aphasia: in cases of brain pathology, language can be disturbed in two rather different ways: as a lexical/semantic system (Wernicke-type aphasia) and as a grammatical system (Broca-type aphasia).

Both language systems not only depend upon different brain areas (temporal and frontal) but also are based on different types of learning (declarative and procedural) supported by different neuroanatomical circuitries. Grammar may be correlated with the ability to represent actions. This is an ability that depends on the so-called Broca's area and related brain circuits, but also depends, is correlated, and likely appeared simultaneously in human history with the ability to rapidly sequence articulatory movements (speech praxis).

Language as a lexical/semantic system may have appeared long before language as a syntactic system, whereas language as a grammatical system may have appeared relatively recently [38,43,101,137,149,150] and seems to be exclusive to *Homo sapiens*. Probably, language grammar represents the departing ability for the development of the executive functions and is based in the ability to internally represent actions.

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