

## BRAIN ANATOMY AND THE ORIGINS OF LANGUAGE

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Language has been considered to be closely related to the concept of human uniqueness for several reasons; among them, its relation to mental processes and the fact that it occurs only in the human species. Since the very beginnings of evolutionary theory, there has been controversy as to whether natural selection can or cannot have produced human language as a result. According to recent studies on the neuroanatomy of the language areas and on brain activation in linguistic tasks, the neural networks involved in linguistic communication appear as part of an overall, macroscopic network of corticocortical connections that serves to handle multiple items of immediate and mnemonic sensory information to be used in cognitive processing. Seen in this light, the neural basis of language corresponds to a specialization of a preexisting neural network whose elaboration is perfectly compatible with natural selection. One additional issue that needs to be investigated is the relation between the increase in brain size and the development of cognitive and social skills in our species. Interestingly, most significant cultural advances have occurred after our brain acquired its present size, perhaps indicating that, for a complex culture to occur and be transmitted to successive generations, some cognitive and linguistic threshold had to be crossed that may relate to the acquisition of a fully generative grammar.

### INTRODUCTION

Besides other anatomical features such as the erect posture, our species is characterized by the capacity for language, which in the majority of people tends to be lateralized to the left hemisphere of the brain. This capacity has been a matter of evolutionary controversy since the very beginnings of evolutionary theory. Although Darwin postulated the origin of man through natural (sexual) selection, the co-discoverer of this process, Alfred Russell Wallace, argued that the origin of man needed some divine intervention (Richards 1987). Even though most people today accept the evolutionary origin of humans, Wallace's argument is still sound. He had the opportunity to meet some aborigines of the Malay archipelago and teach them how to read, write and do arithmetics. Wallace reasoned that if these aborigines had never been exposed to written language or arithmetics, they could not have evolved the capacity to learn these skills through gradual steps as required by natural selection. The solution to this problem may lie in the fact that these aborigi-

nes already had spoken language and therefore they managed the basic rules of syntax and logic that permitted them to learn other forms of symbolic communication.

The more modern structuralist approach, championed by Noam Chomsky (1978), also denies the origin of language through natural selection as long as there is no evidence of any precursor of the generative properties that are essential to our grammar. A more recent perspective (Pinker and Bloom 1990) argues that syntactic rules may have originated through the accumulation of small, successive steps as required by natural selection. In addition, it has been proposed that the acquisition of linguistic rules corresponds to specialized learning patterns (which can be genetically determined) rather than to the direct expression of innate characteristics, as the Chomskyan perspective implies (Aboitiz and García 1997a). In other words, the genetic basis of language may better correspond to inherited rules of plasticity and learning rather than to the representation of syntactic rules in the genes.

Although brain lateralization of functions is usually associated to language, neuroanatomical and neurocognitive evidence indicates that the human brain is not the only one to be lateralized. In primates and other animals distinct degrees of brain asymmetry have been detected even in regions corresponding to language-related areas in the human (Bradshaw and Rogers 1992, Gannon et al. 1998). This and other evidence suggest that specific neural precursors of language-related regions exist in other species, differing from the human condition more in quantity than in quality. On the other hand, considering the high degree of encephalization (brain size in relation to body size) of hominids, the most frequent assumption is that language origins are somehow associated to the increase in brain size. However, human brain size has remained constant in the last 100,000 years, with a tendency to decrease in the last 10,000 years (Henneberg 1992, Stanyon et al. 1993), while archaeological evidence for a complex representational capacity, such as seen in rock art, goes back to no more than 50,000 years (Noble and Davidson 1996).

Therefore, the issue of the origin of language (and the origin of what is uniquely human) still poses several unanswered questions such as (i) is language the result of natural selection?, (ii) in what sense can it be argued that there is a genetic basis for language?, (iii) what is the difference between our brain and that of the rest of primates besides the difference in size?, and (iv) is there or is there not a relation between brain size and our linguistic capacities? Although, admittedly, we may still have to wait a long time to have straight answers to these questions (though we may be about to witness many interesting advances; see below), my intention in this article is to propose a perspective that is based on recent neuroanatomical evidence. This implies a gradual origin of language, based on the natural (sexual?) selection of subjects with a higher capacity for working memory, which can be traced back to precursor elements such as the widespread temporoparieto-prefrontal connections in the primate cerebral cortex. Part of these arguments (mainly addressing points i, ii and iii above) have been elaborated at full length in

other recent articles (Aboitiz and García 1997a, b). Here I will summarize some aspects of this proposal and will add some original considerations regarding point (iv). I will also deal with some issues that, in my view, hold the greatest promise for future neurolinguistic research.

### 1. THE ORIGIN OF LANGUAGE FROM A WORKING MEMORY NETWORK

As mentioned, Aboitiz and García (1997a, b) proposed that the neuroanatomical substrate for language (consisting of a posterior Wernicke's area —related to area Tpt— connected with an anterior Broca's area —related to Brodmann's areas 44/45— via the arcuate fasciculus; see Fig. 1) has important similarities to widespread neural networks connecting temporoparietal and prefrontal regions. Such networks participate in what has been denominated 'working memory' (Baddeley 1986), a kind of short-term memory that permits to maintain "on-line" cognitive and sensory information that is being used for immediate or for short-term behavior. Working memory can be of

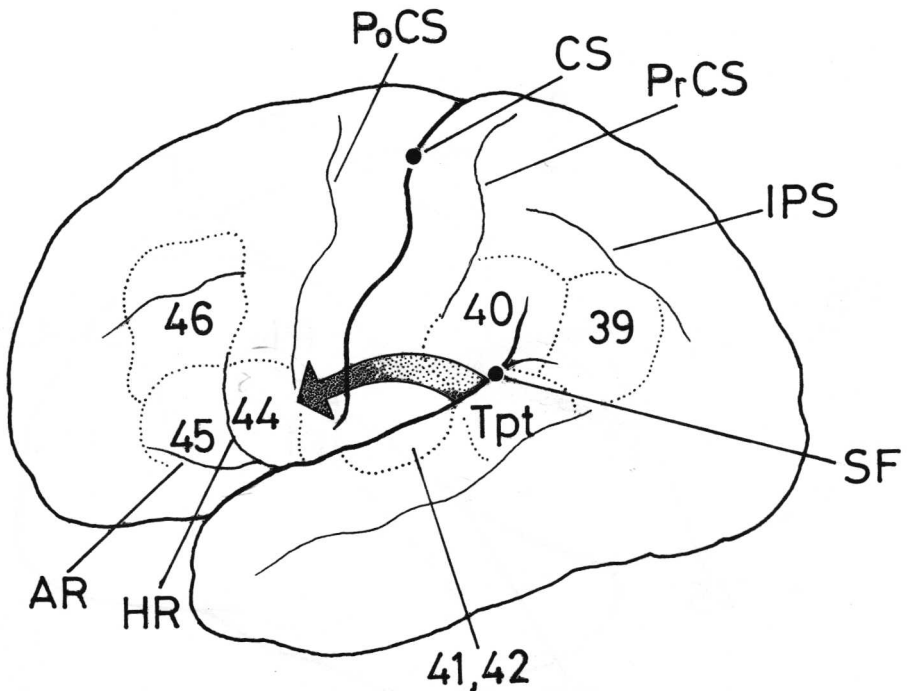


Fig. 1: Diagram of a human brain showing the location of the areas described in this article. Broca's area corresponds to Brodmann's areas 44/45, and Wernicke's area has been proposed to correspond to area Tpt. The arcuate fasciculus (curved arrow) has been proposed to connect Broca's and Wernicke's areas. AR, ascending ramus of the pars triangularis; CS, central sulcus; HR, descending ramus of the pars triangularis; IPS, intraparietal sulcus; PoCS, postcentral sulcus; PrCS, precentral sulcus; SF, sylvian fissure.

several kinds, one of them being linguistic (short-term memory for linguistic items).

The neural systems that participate in such kind of working memory correspond, to a large extent, to the language areas and their connections. Of particular interest is the supramarginal gyrus that contains area 40 (Fig. 1), which has been claimed to transiently store a phonological representation to be posteriorly rehearsed in the anterior Broca's area (Paulesu et al. 1993, Salmon et al. 1996). Lesions in area 40 have also been reported to produce conduction aphasia, which consists in the incapacity to repeat linguistic utterances presented to the patient (Alexander 1997) and can be described as a deficit in working memory for language. No direct homologue of area 40 has been described in the monkey, but inferoparietal regions that topographically correspond to this area are known to project to the equivalent to Broca's area (Fig. 2).

Moreover, the region that has been assumed to correspond to Wernicke's area in the superior temporal lobe does not project to Broca's region but to frontal granular sectors located in the dorsolateral prefrontal cortex (Fig. 2).

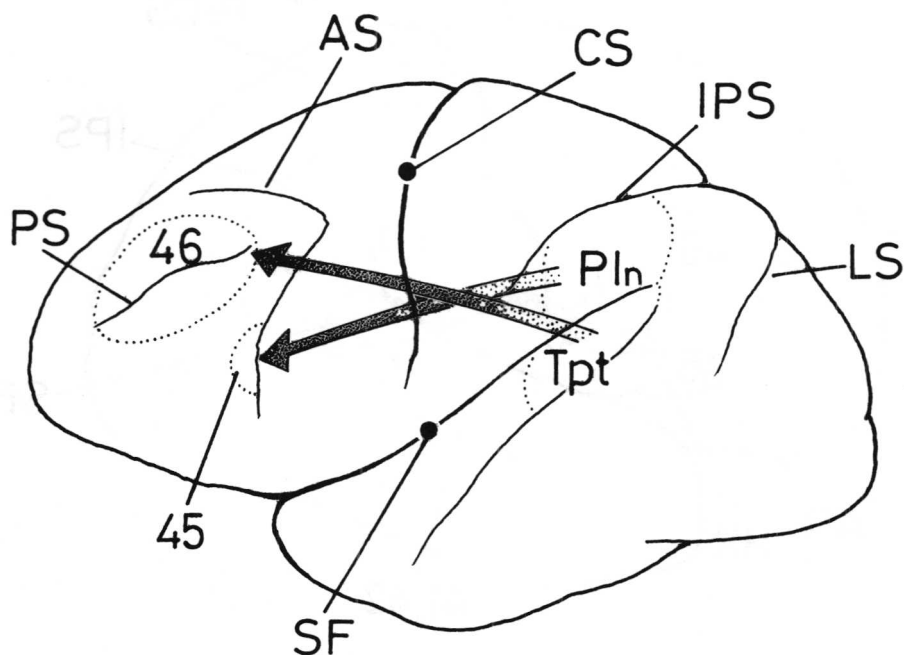


Fig. 2. Connections between area Tpt (related to Wernicke's area in the human) and the superior frontal lobe (area 46), and between the inferior parietal lobe (Pln, perhaps related to area 40 in the human) and area 45 (related to Broca's area in the human) in the monkey.

Thus, the anatomy of the language regions may not be so simple as a direct projection from Wernicke's to Broca's areas, but may rather involve parallel projections from inferoparietal areas to Broca's area and from Wernicke's area to dorsolateral prefrontal cortex. There is the possibility that a direct projection from Wernicke's to Broca's region developed in the human lineage, but nevertheless the involvement of inferior parietal sectors and of dorsolateral prefrontal regions in language is evident from imaging and lesion studies.

The circuit involved in linguistic working memory therefore fits closely the anatomy of the language areas in the brain. We (Aboitiz and García 1997a, b) have postulated that the language areas originated as a specialized working memory device for transiently storing and retrieving complex phonological utterances that were of behavioral significance in the complex social system of primitive hominids. Such complicated phonological sequences were probably learned by imitation in infancy and became increasingly complex as the social interactions were more elaborate. (A scenario somewhat similar to this has also been proposed by Lieberman 1991.) A sophisticated working memory system became necessary in order to produce a sensorimotor loop that internally rehearsed these utterances while they were learned. This sensorimotor loop eventually differentiated as an anatomically delimited system, defining a primordial language apparatus in the cerebral cortex. Progressive interaction between this incipient language device and other regions in the posterior, sensory and association cortices, and also with other prefrontal areas (particularly dorsolateral prefrontal cortex) permitted the generation of a complex reference system to objects and actions, establishing a primitive lexicon and its associated syntactic rules.

## 2. THE GENETICS OF LANGUAGE

One main point outlined in the previous section is that the generative capacity for language, as well as the presumed universal syntactic rules, may represent characteristics and constraints that correspond to the dynamics of neural interactions between macroscopic networks involving temporal, parietal and prefrontal cortices. In other words, universal rules probably reflect the dynamics of the interface between purely cognitive systems and the specialized language processing device that is partly located in the so-called language areas. These interactive domains are genetically determined in the sense that any plastic structure in the brain needs a genetic framework to be built. That is, circuits involved in learned tasks always require a basic, genetically-determined repertoire of connections (Edelman 1987) that becomes elaborated during the process of learning. It is very likely that in the human brain there is a genetically specified, basic repertoire of connections that permits the generation of syntactic rules through the elaboration of such circuits during the exposure to other speakers. However, this is, in my view, very different from stating that the structure of language is in some way innate. Although the Chomskyan argument of the poverty of stimulus (which states that the samples of language that children are exposed to are not complex enough to

account for the richness of their language) has been widely claimed, evidence to date is by no means strong enough to support it. In order to substantiate the claim that there is an innate knowledge of syntax, there should be strong results indicating that language can develop autonomously, but these data are nonetheless elusive (Seidenberg 1997). In fact, it is not at all clear as to what extent children are capable of mastering syntactic rules without proper exposure to them. In my view, the Chomskyan approach has failed to provide adequate evidence that the linguistic stimuli presented to children are insufficient for the development of a syntax through a learning process.

Evidence for genes involved in language has been elusive to date. *Handedness* (which is related to certain aspects of language lateralization) is believed to be partly genetically determined (Galaburda and Aboitiz 1986). More direct evidence is the familial character of language-related disorders such as dyslexia and specific language impairment, although there is controversy as to whether this condition reflects a simple etiology (Gilger 1992, 1995, Bishop 1994). Recently, some genetic defects have been associated with language development such as the Williams syndrome, which results from a deletion in chromosome 7 (Lenhoff et al. 1997) and, among other things, is characterized by a remarkable preservation of the linguistic and musical capacities despite a subnormal general intelligence. Other candidates are a recently discovered gene, also in chromosome 7, which produces an incapacity to coordinate the musculature required for appropriate speech (Fisher et al. 1998), and a gene possibly located in the sexual chromosomes, X and Y (Crow 1994), whose presence may produce a bias in brain development, favouring right-hemisphere characteristics (or perhaps impairing the development of left-hemisphere characteristics).

The search for the genetic basis for language is still in its beginnings and the results, although sometimes provocative, still need to be confirmed in many of the cases. Nevertheless, in my view, we are now on the threshold of a new era for linguistic studies: new brain imaging techniques will allow us to study in great anatomical detail the brain regions involved in specific linguistic tasks, and powerful molecular techniques may permit a careful genetic dissection of linguistic behavior.

### 3. IS BRAIN SIZE RELATED TO LANGUAGE?

I have proposed before (Aboitiz 1996) that there are two different modalities of increase in brain size in evolution: the most common, passive growth, occurs as a consequence of generalized increases in body mass. The brain is one more organ in the body and is not exempt from the regulation of cell proliferation that occurs in the rest of the animal. So, if the animal becomes bigger, the brain also becomes bigger. This type of growth is not necessarily associated with increases in brain processing capacity. The second type, active growth, is brain growth that results from selection for processing capacity. In this type of growth, the most important point is the generation of neuronal rearrangements that will produce increased plasticity, more refined neuronal

maps, etc. Increase in brain size results in more brain space to perform such rearrangements and is therefore favored by natural selection.

However, in the case of humans, evidence indicates that the relative size of the cerebral cortex does not deviate dramatically from the proportions observed in primates. That is, although we have a larger neocortex, and even a larger proportion of neocortical tissue than other primates, this increase is what is to be expected for a primate with a brain the size of ours. Our cortical development follows the trend observed in all primates toward increasing the relative amount of neocortex. The development of specific cortical areas may, however, differ in humans in relation to other primates. The prefrontal cortex (located in the front of the brain and related to the control of complex behaviors and impulses) is a controversial case. It has been claimed that the prefrontal cortex is particularly developed in the human brain, especially a region denominated granular frontal cortex that contains area 46 (see Fig. 1) (Preuss 1995). However, Jerison (1997) has argued that in humans the prefrontal cortex follows typical primate trends. He claims that, although our prefrontal cortex is larger, even in relative terms, than that of other primates, its size corresponds to what is expected for a primate with our brain size. (However, Jerison plotted prefrontal cortex volume against total brain size; the latter includes as a significant component the size of prefrontal cortex itself, which may have artificially minimized the differences between humans and other primates). Deacon (1990) has reported that humans dramatically diverge from other primates in terms of the relative proportions of association versus sensory/motor cortices, and of the relative volume of laminar (cerebral plus cerebellar cortices) versus non-laminar structures (rest of the brain). More recently, Holloway et al. (1998) also indicate that the relative size of human primary visual cortex is quite diminished in humans relative to other primates, being less than expected for a primate with our brain size. This suggests that in the human lineage a significant reorganization of the posterior parietal and temporal lobes has taken place. This concept is consistent with comparative analyses of the visual cortices in primates, showing differential development of the color-sensitive area V4 in nocturnal and diurnal primates. This produces as a consequence diverse topographical arrangements of other visual areas like the motion-sensitive area MT (Kaas 1993). Likewise, changes in the relative development of particular areas may well have taken place in the hominid lineage.

On average, primates have a brain that is about twice as big as that of other mammals (there being an important degree of overlap), and that morphologically is characterized by a large temporal lobe and a prefrontal cortex. The concomitant expansion of these two lobes (plus the insular lobe) relates to the development of macroscopic neural networks connecting all these brain regions. The increased brain size and more complex connectivity of primates probably relate to the complex social lives these animals have. Although in society there is the benefit of cooperation, to an important extent there is competition among individuals to obtain resources of different kinds, from food to access to members of the other sex in order to reproduce. In



other words, although by being a member of the society the individual may passively gain access to some resources, the more assertive he is the more benefits he will obtain. Therefore, there is a good prize in actively seeking resources and competing with other individuals. One current interpretation proposes that the capacity to interpret other individuals' intentions, anticipate their moves, and to plan how to obtain different types of resources while competing with others was a fundamental requirement for brain development in primate and especially in human evolution (Cosmides and Tooby 1995). A related requirement for a complex and competitive social life is the capacity to maintain awareness of several sources of information in order to behave appropriately and be able to take advantage of the circumstances. For this, working memory may have been a crucial element as it permits the transient storage of behaviorally relevant information so that it may be rapidly retrieved at the right time. Therefore, in primate evolution there may have been a strong selection for the ability to interpret the behavior of others, for an elaborate cognitive system including a powerful working memory in order to maintain awareness of the social dynamics and the availability of resources, and finally for the elaboration of a system that controls impulses according to the social circumstances. All these behaviors required the development of a complex cortical network involving at least prefrontal, orbitofrontal, insular and temporoparietal regions. Probably, a correlated development of all these and other parts—and more importantly, the development of macroscopic neuronal networks linking all these regions—resulted as a consequence of selection for these abilities. It is also very likely that in the human lineage the same or very similar abilities as those selected in other primates were selected for, which resulted in the further enlargement of the brain as a whole. Below, I will argue that the origin of language, which of course required a sufficiently large brain and a powerful working memory device, was also fundamental in the sense that it fueled the further development of cognitive abilities and the capacity for social awareness.

As mentioned before, we (Aboitiz and García 1997a, b) have proposed that the language areas in the human brain originated from a network for short-term memory and rehearsal of complex phonological utterances. This capacity probably required a sufficiently large brain in order to develop. However, a perhaps more important aspect was that when these utterances became capable of signifying objects, places, behaviors and attitudes, the proper states of mind of each individual became more evident to others. In other words, language (or protolinguistic utterances) permitted to unveil the state of awareness and the cognitive capacities of the different members of the group. In other words, through the use of linguistic communication (which does not necessarily imply a fully developed language), individuals could be labeled by others according to their cognitive (and also linguistic) abilities, which gave them different positions in the social environment and hence partly determined the subjects' access to members of the other sex. Put simply, the point of this argument is that if you are dumb, you are better off with your mouth shut. Once you begin to talk, others will realize how dumb or clever



you are and will start discriminating against you one way or another. This scenario implies that, although linguistic capacities required a large brain to originate, they also intensified the selective trend toward increased cognitive abilities such as those required for successful behavior in society, a trend that, as pointed out before, has been present in the whole history of the primate order. In this sense, perhaps it should be no surprise that the human brain does not diverge in some of its proportions from the tendencies observed in the rest of the primates.

One remaining question is that, as stated above, most significant cultural advances have occurred in the last 50,000 years of human evolution, period in which the brain was already the size of that of modern humans. Therefore, our large brain was originally perfectly capable of much more than it was originally selected for. Cultural advances are the result of learned capacities, not inherited ones, and the human brain is the result of selection for a powerful memory and learning capacity. Perhaps in this respect our children are not different from the earliest humans. In this sense, the human brain is an organ specialized for cultural learning, which requires a good memory system, learning capacity and especially the ability to master language. Therefore, language may be considered as a requisite for an efficient process of cultural transmission. One possible explanation of why brain size appears decoupled of cultural advances in the history of hominids is that language was not fully mastered until relatively recently. Perhaps the development of linguistic capacities that, as said above, brought with them a strong natural and sexual selection for cognitive ability, only recently reached a threshold on which social learning was capable of sufficiently complex transmission such as that required for developing primitive civilizations. When the lifestyle became more comfortable through cultural advances, selection for cognitive and linguistic capacities relaxed, yielding a stable brain size in the last periods of human history.

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