A BRAIN FOR SPEECH

A View from Evolutionary Neuroanatomy

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I dedicate this book to my wife Carolina and to my children Sebastián, Gabriel, Camila, Simón, Martín, and Antón. Their love has been a main motivation to write this book.

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Before Reading This Book

This is a book on brain evolution that focuses on the human brain and the origin of speech and language, which as will be seen in the book, are not exactly the same. It is primarily directed to graduate and undergraduate students of areas related to neuroscience, psychology, linguistics, and biology and to anybody interested in the evolution of the brain and language. The book has a strong neuroanatomical content, as this has been my personal field of interest throughout my career. In addition, historical issues permeate practically all chapters, in three different dimensions. One of these is biological evolution, which explains how we came to be as we are. Like any historical process, evolution does not follow a predetermined path, but is full of accidents and contingent situations that make the process much less smooth and more intricate than we could imagine at first consideration. Nonetheless, evolution is usually a gradual process, and therefore many times it is possible to find evidences of intermediate stages in the acquisition of different features, including language. A long linguistic tradition has maintained that language is so different from any other form of animal communication that it must have appeared all at once. Here, I will argue for a continuous transformation of the brain and its circuits in human evolution, which led to a brain capable of speaking and using language. I will look through the lens of comparative neuroanatomy, where evidence for continuity is, in my view, quite strong.

The second historical dimension is that of science. Science, and especially evolutionary theory, advances through controversies, sometimes very agitated. I have tried here to provide a glimpse of the discussions that have taken place in the search for human and language origins to illustrate that many of the arguments in which we are presently engaged have their roots in our deep history. Controversies in science are not supposed to be resolved by brilliant arguments, but rather by straight evidence. Unfortunately, in many cases, this evidence has been hard to find, and this has fueled intense research programs that, although providing much knowledge, in many cases have not provided clear-cut answers to really important questions. Many current ideas are shaped by much of the earlier thoughts of brilliant researchers that have been left to oblivion. As a prestigious journal editor once mentioned to me, sometimes people seem to believe that the field they work in did not exist before Internet.

Finally, the third perspective is my personal history. Throughout this book, I discuss the topics that have been of my own interest and in which my students and I have contributed with data and hypotheses. As I said, the main thread in this history is evolution, particularly of the human brain. Being anthropocentric, language can be seen as the epitome of biological evolution, and its origins deserve study. This is reflected in my early research in the laboratories of Humberto Maturana and Francisco Varela in Chile, then Albert Galaburda in Boston, and finally Eran Zaidel and Arne Scheibel in Los Angeles, California, where I did my doctoral thesis studying the neuroanatomical aspects of brain asymmetry and interhemispheric communication. Besides this, I became interested in other aspects of brain evolution, like the acquisition of a large brain size and the origin of the cerebral cortex, a character found only in mammals. In several chapters, I discuss my own work on these lines, attempting to provide a deep evolutionary perspective to the human brain, which I hope may provide useful insights into our self-knowledge.

The book is divided into two parts. The first, “A Special Brain”, covers some characteristics of the human brain like the language-specific network (Chapter 2), the size of the human brain (Chapter 3), its lateralization of functions (Chapter 4), and interhemispheric integration

(Chapter 5), and a cognitive capacity called working memory, especially a circuit termed the "phonological loop" that I argue was a key innovation in human evolution (Chapter 6). In the second part, "Before Speech", I discuss the neuroanatomy of the monkey brain, trying to find the ancestry of the language networks (Chapter 7). Next, I critically discuss research on mirror neurons, which have been proposed to account for language origins in humans (Chapter 8); and on songbirds and vocal learning birds like parrots, which are used as models for human speech acquisition (Chapter 9). After this, I address emergent evidence of vocal learning capacities in mammals, which are phylogenetically closer to humans (Chapter 10), and the ecological and social context in which speech evolved in our early ancestors (Chapter 11), in order to provide a coherent picture of language and the evolution of other aspects of human behavior. I hope this book will motivate young researchers to pursue work and develop further testable hypotheses along these lines, which in my opinion represent the most fundamental questions of our own existence among the seemingly endless variety of life forms on this planet.

Contents

List of Abbreviations

A	auditory area
AC	anterior cingulate cortex
AI	anterior insula
AIP	area intraparietalis
AF	arcuate fasciculus
AM	amygdala
ATL	anterior temporal lobe
B	Broca's area
CC	corpus callosum
CP	cortical plate
C-R	Cajal-Retzius cells
CX	cerebral cortex
CVC	consonant-vowel-consonant
DLM	dorsal lateral nucleus of the medial thalamus
DLPF	dorsolateral prefrontal cortex
DMN	default mode network
DTI	diffusion tensor imaging
EC	extreme capsule
EEG	electroencephalography
EQ	encephalization quotient
ERP	event-related potentials or evoked potentials
FAT	frontal aslant tract
fMRI	functional magnetic resonance imaging

He	cortical hem
HM	Henry Molaison
HP	hippocampus
Hy	hyperpallium
HVC	Nucleus HVC of the songbird brain
ICo	nucleus intercollicularis
ILF	inferior longitudinal fasciculus
IZ	intermediate zone
L	field L of the songbird brain
LC	laryngeal cortex
LGN	lateral geniculate nucleus
LMAN	nucleus LMAN of the songbird brain
M	mesopallium
MGE	medial ganglionic eminence
MLF	middle longitudinal fasciculus
MPF	medial prefrontal cortex
M	motor cortex
MRI	magnetic resonance imaging
MT	area MT
M1	primary motor cortex
N	nidopallium
NA	nucleus accumbens
nXIII	XIII cranial nucleus
OF	orbitofrontal cortex
Ol	olfactory cortex
PAG	periaqueductal gray
PAR	parietal lobe
PC	posterior cingulate cortex
PET	positron emission tomography
PFG	area PFG of the inferior parietal lobe
PP	planum parietale
PS	pial surface
PT	planum temporale
Q	optic chiasm
RA	nucleus robustus archistriatum of the songbird brain
RG	radial glia
SLF	superior longitudinal fasciculus
SLF I	dorsal superior longitudinal fasciculus

SLF II	middle superior longitudinal fasciculus
SLF III	ventral superior longitudinal fasciculus
SMG	supramarginal gyrus
SP	subpallium
SPECT	single photon emission tomography
STS	superior temporal sulcus
SVZ	subventricular zone
TC	tectal commissure
TE	visual area TE
TMS	transcranial magnetic stimulation
Tpt	area Tpt in the planum temporale
UF	uncinate fasciculus
VE	ventricular epithelium
VLPF	ventrolateral prefrontal cortex
VM	ventromedial cortex
VOF	vertical occipital fasciculus
VZ	ventricular zone
V1	primary visual area
V2	secondary visual area
W	Wernicke's area
X	area X of the songbird brain

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Introduction: The Beginning of Words

If alien visitors were to come to earth, there is little doubt that we would be the first species they noticed as they approached from space. After all, we are the only animals that have managed to leave our planet and adventure into outer space, sending robots to other planets and placing a probe on the surface of a nearby comet. Few if any changes in the history of life have been as radical as the ones we are imposing with our technological capacity, changing the shape of the biosphere in a geological instant. Thus, there is no doubt that our species is vastly different from all others in the ability to alter the environment for our immediate benefit. Furthermore, this is largely due to our unique ability to communicate through language. Language enables a mental or semantic space that we share with others and helps us to coordinate our behavior, anticipate the future, describe the world around us, imagine utopic scenarios, and manipulate our surroundings. Language is expressed in a variety of forms, the most obvious being speech, but we also use language for reading and writing, and some use sign language. Some claim that language first arose in the form of hand gestures that were later overtaken by the elaboration of speech, while others, including myself, are more comfortable with the notion that speech was the first

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way to express modern language. In any case, our capacity to communicate has made us perhaps the most successful animal species, which is the signature of biological adaptation. Our present nature is inseparable from our language. How our ancestors came to acquire language is therefore a fundamental evolutionary and social question that touches on our very nature and, as I believe, can give us useful information on how to survive as a species.

This book is concerned with the key neurobiological steps that allowed us to start the language explosion that changed our lives forever, which for all we know does not show signs of having ended. It is commonly said that we are genetically 98.6% similar to our closest relative, the chimpanzee, so this extraordinary impulse must have been caused by only a few mutations that reorganized our brains and our capacity to understand the world, to communicate with others, and to manipulate our environment. These changes may have been caused by classical genetic mutations, possibly in so-called regulatory genes that work as master organizers of large-scale developmental processes. Mutations in these genes may have been important in producing rapid changes in the overall structure of neural networks or in rapidly increasing brain size. One example of these genes may be FOXP2, whose mutations have been associated with certain forms of speech disorders. In addition, recent research has called attention to epigenetic modifications that are acquired but lasting alterations in the patterns of expression of some genes. At the behavioral level there are cultural modifications that can influence the plastic development of the brain, producing connectional rearrangements in ways we do not yet completely understand, and which may have contributed to rewiring our brains for language. One intriguing possibility is whether epigenetic mechanisms are influenced by cultural transmission. Although research on these lines is fundamental, one problem with genetic studies of language capacity is that they do not tell us what the phenotype is, or precisely which anatomical and functional characteristics allowed us to develop speech, and eventually language. In my opinion, this is the most critical question of language origins, and all others, including genetic, cultural or linguistic accounts, will eventually have to be subordinated to an explanation of how our brains construct language.

Before continuing this discussion, it will be useful to clarify some basic definitions, so that we can agree about the terms I will use. First, what is language? Human language differs from other forms of animal and human communication in its internal structure, which is organized in several components. Human language has syntax or grammar, a lexicon or set of words, and semantics or meaning. For modern linguists and other specialists, language is not equivalent to speech. Speech is a particular way to express language, as there are also sign and written languages. Furthermore, spoken language has phonology, which refers to the articulation of different sounds (phonemes) to make up larger meaningful units (morphemes, that are words or parts of words), and prosody, which relates to the intonation patterns and emotional contents we transmit during speech. Other forms of language, like sign language, have an equivalent of phonology and prosody, while written language relies on auditory representations that contain phonological and some prosodic features. Finally, associated with language are other elements like its pragmatics, or the social context in which language operates, and related cognitive abilities like mathematics and of course music, which Charles Darwin said was closely related to speech in its origins.

While the more abstract notion of language has been the subject of interest for most linguists and some biologists, in this book I will focus rather on speech. The latter is an observable behavior that includes clear functional and morphological adaptations, making it more amenable to a biological approach. Furthermore, in recent years there has been a tendency (with some notable exceptions) to downplay the importance of speech in language origins in favor of hypotheses that consider speech as a secondary achievement. Throughout this book, I will speak of language when referring to more abstract aspects of human communication, and to speech when referring to the specific sensorimotor system involved in speech production. Sometimes, I will refer to language and speech to emphasize that I am speaking of both the vocal-sensorimotor and the abstract components of language. My interest in this book is to highlight speech as a fundamental element in the origin of modern language and to depict an educated scenario for the evolution of the neural circuits involved in its generation. For this purpose, I will explore the evolutionary history of our brain to understand from where these networks originate.

Darwin, Broca and the Human Brain

Perhaps the most basic assumption we need to make before continuing is that the human brain is the product of biological evolution and that the origin of language is inevitably related to the evolution of the human brain. In the mid to late nineteenth century, Charles Darwin's ideas on evolution sparked intense debate, not only with the church, but also within science. Darwin first published his *Origin of Species* in 1859, and in 1871 he published the *Descent of Man*, in which he argued that humans and apes had a common ancestry, and also proposed a biological origin of human language (Darwin 1859, 1871). On this point he dissented from the co-founder of the theory of evolution, Alfred Russell Wallace, and with the main linguistic tendency of the time, which viewed language and the human mind as attributes unique to the human species. Darwin proposed three stages in the acquisition of human speech or language, first a general increase in intelligence that permitted more complex social behavior and a primitive kind of thought, which was followed by the development of complex vocal control in the form of primitive melodies, a "musical protolanguage" as termed by Tecumseh Fitch (Fitch 2010). Subsequently, these melodies achieved meaning by imitating natural sounds, aided by signs and gestures.

However, Darwin never directly addressed the issue of brain evolution, or whether the human brain evolved gradually from that of non-human primates. On the other hand, Richard Owen (Owen 1837; Desmond 1984), Darwin's main scientific opponent and arguably the most brilliant anatomist of his time, pointed to apparent key differences between the human brain and that of non-human primates. Instead of believing in a historical transformation of species, Owen believed in an ideal, abstract world where forms or species existed immutably. Owen was also a strong defender of man's privileged place in nature and published several works highlighting the uniqueness of the human brain. In 1857, two years before Darwin's *Origin*, Owen published an article indicating characters apparently unique to the human brain, namely the so-called calcar avis or hippocampus minor, which is a small groove in the posterior horn of the lateral ventricle (now known to be associated with the development of the calcarine fissure, which contains the primary visual area) (Gross 1993). In addition, the development of the posterior lobe of the brain, associated with the enlargement of the posterior horn of the lateral ventricle, was also considered to be a uniquely human attribute. Both features endowed humans with their supreme power over all other animals and creation. Owen illustrated this point by comparing the brains of a gorilla and a "negro", the former supposedly lacking these characteristics. While Darwin made only mild commentaries on Owen's statements, his close follower Thomas Henry Huxley (nicknamed "Mr. Darwin's bulldog") defended him against Owen and the church's opposing creationism. On this particular issue, Huxley demolished Owen by quoting other authors that showed the presence of a calcar avis in several animals including non-human primates (Gross 1993). This pointed to a gradual transformation of the brain from apes to humans. Still, the question remained, what was in our brains, and not in those of apes, that made us speak?

Another character of relevance for our purposes is Pierre Paul Broca, a brilliant physician, surgeon, and anthropologist contemporaneous to Huxley (Broca was only 1 year older), who embraced the notion of human evolution (Schiller 1992). He has been quoted as saying that he preferred being an evolved ape than Adam's degenerate descendant. However, although he agreed that it was a splendid hypothesis, he insisted on the lack of evidence to support the theory of evolution by natural selection. In 1859, Broca founded the Society of Anthropology of Paris, which was dedicated to the study of the human races, their origins, and their evolution. Two years later, Broca presented the case of a patient with a localized lesion in the brain that had lost the ability to speak, a crucial finding that initiated the study of the neural basis of language and established that speech was the product of specialized structures in the human brain (see Chapter 2). In addition, Broca made important contributions to physical anthropology, analyzing the cranial shapes of different European groups and attempting to trace European – and French – ancestry. The first formal paper from the Society of Anthropology was of his authorship, in which he argued that the French were in fact a mixture of peoples, at odds with the widespread notion that the French were a single race derived from the Celts. An important part of his anthropological work consisted of a craniometric analysis of Basque skulls, as compared with skulls from northern France. Although Broca believed in a separate origin of the human races, he also firmly argued that the mixing of races was not detrimental to their vigor or intelligence, which challenged the contemporaneous notion of the superiority of "pure races" like the Celts or Aryans. Broca also did some paleoanthropological work, notably describing the skull and skeleton of the Cro-Magnon man found in the region of Les Eyzies in southern France, and the study of ancient trephined Peruvian skulls.

Did Language Evolve?

While the notion of human evolution was slow to be accepted, ideas about the origin of language and speech were debated long before Darwin's evolutionary theory. However, it was only after him that these traits began to be considered a biological issue. In *The Descent of Man*, Darwin asserted that speech owes its origin to the capacity to imitate and modify natural sounds, as well as the voices of other humans and other species (Richards 1989). He emphasized the coevolution of music and language, arguing that the earliest languages were musical, and claimed that language evolution was closely aided by the development of communicative gestures. With his characteristic insight, he went on to propose that the process of speech acquisition was not much different from the mechanism of song learning in songbirds. However, Darwin was not alone in his interest in the genesis of speech. Nearly contemporaneous to the publication of Darwin's work, there was an avalanche of ideas on the origin of language, including proposals of imitation capacity, emotional exclamations, rhythmic behavior, and gestural communication. Among the most influential of these theories was that of Gottfried Herder (Herder 1800), who proposed that the first words were imitations of natural sounds, like the onomatopoeias of modern languages (words that recall natural sounds like "oink", "meow", "buzz", etc.). Another theory was that innate calls like crying or laughing served as the substrate for the origin of words, as these calls convey socially important emotional information. Grunts and other calls gradually transformed into primitive words, or proto-words as they are called. In a similar line, James Burnet proposed that innate cries became varied by musical tones before becoming articulated words. This hypothesis implied that speech derived from music, which was considered to be a more primitive form of expression. However, the neurological findings at the time, showing dissociation between speech capacity and emotional expression, were used as firm evidence against this hypothesis. Finally, the prestigious philosopher Étienne de Condillac supported the notion that language originated as gestural communication, akin to the sign communication used by the hearing impaired (Richards 1989; Fitch 2010).

All these theories had one thing common: none had a single bit of evidence in their support. They were all speculations about our early history. In 1866, the *Societé de Linguistique de Paris* decided to ban this sterile discussion from academic contexts, producing a long eclipse in research about language evolution. Fitch asserts that the linguist Friederich Max Müller was perhaps the most radical opponent to theories of speech origins (Fitch 2010). He rejected the most well-known theory of onomatopoeia on the grounds that most words are not strict imitations of sounds. However, this imperfect imitation can be sufficient for others to match the vocalized sound to the natural sound it refers to. It does not need to be perfect to communicate its meaning. Müller acknowledged that humans could have evolved from other species, but in agreement with the Book of Genesis, he believed language to be a gift from God, who gave humans a single language that diversified into all extant languages. Müller's research focused on the reconstruction of the original human language, a subject on which he had been a pioneer, and in this respect considered himself to have been a "Darwinian before Darwin". However, the original language was to him an abstract entity, a machine for thought, not a concrete system of sounds. On this, he joined the idealist tradition that has continued into modern linguistics.

Even if at first sight the arguments proposed at that time sound naïve, all these proposals remain important in the literature of language acquisition and evolution. To be fair, although we have acquired tremendous knowledge of linguistics, biology, anthropology, and psychology, the main question of why we were the only species to acquire language, and the specific process underlying this transformation, remains unsolved. This may not be anyone's fault, given that language and behavior, unlike other biological characters, do not leave fossil traces, and we cannot know directly how our ancestors communicated. Moreover, despite our genetic similarity, non-human primates show nothing remotely similar to language or speech, and there are no living human-like species using a primitive form of communication that would help in tracing the history of language acquisition.

Deep Structures

In the second half of the last century, the extraordinary linguist Noam Chomsky (well known to the general public for his radical anarchistic declarations) and biologists like Richard Lewontin (Chomsky 1957; Lewontin 1975) further contributed to dismissing the evolutionary origins of language by boldly claiming that language was so unique that it was not explainable by evolutionary theory. Excluding notable attempts by a few twentieth-century neurologists and psychologists, scientific enquiry into the origins of language and speech only re-emerged in the last 20 years by virtue of the advent of neural imaging techniques to assess language processing and brain anatomy, and the development of comparative approaches to non-human species that provided insightful models of the development of communication and other behaviors. There has been much research recently on neural networks and the mechanisms underlying language, memory, and motor control, together with exciting comparative studies on the brains of non-human primates and animals like songbirds that are able to learn new vocalizations. All these studies have yielded important evidence that, although still fragmentary, provide a new avenue to thinking about language and its origins.

Apart from this recent influence, linguistics has traditionally been an issue of paper-and-pencil work, attempting to unveil the logical organization of linguistic utterances. Chomsky's revolutionary theory emerged in this context, claiming that despite their superficial differences, all languages share a deep grammatical organization based on the hierarchical organization of phrase structure (broadly referred to as generative grammar). The acquisition of grammar is considered to be innate, as all humans share the capacity (or competence) to master language. Thus, language has a universal structure and we are endowed with the ability to learn it from birth. Furthermore, the structure of language is considered to be unique, having no parallel in either other human cognitive functions or any animal cognitive or communication system. Chomsky strongly emphasized phrase structure as the key element of language, downplaying other elements like lexicon, phonology, or semantics as less relevant to the essence of language. For Chomsky, language consists of a core computational system that, although useful for communication, represents the fundamental structure of the human mind.

Chomsky made a titanic contribution to formal linguistics. He is probably the best syntactician that has ever lived, and imposed a tough, logical approach to the study of grammar. His influence began with the publication of the book *Syntactic Structures* (Chomsky 1957), which was based on his doctoral dissertation. There, he attacked and practically destroyed the then prevalent view that language was acquired by behavioral mechanisms of learning and associativity, proposing instead that language was the result of an innate capacity. In subsequent works, Chomsky engaged in in-depth analysis of syntactic organization, for which he developed a highly intricate logical system that, although clear to him, became increasingly obscure for non-linguists and even many linguists as well (Chomsky 1965). This whole analysis revealed that the grammatical structure of language could become extremely complex, so much that it required a sort of Copernican revolution to make more sense of it. Attempting to simplify his theoretical construct, Chomsky argued that the essential feature of language is its recursive grammatical structure, which in simple terms is the process of inserting sentences into other sentences, generating an embedded organization where phrase components are hierarchically nested into longer phrases in a potentially infinite branching tree. Recursion, he claimed, is unique to language and is not originally intended for communication, but makes up the architecture of the mind. Going further in this search for simplicity, Chomsky offered "The Minimalist Program", in which he pointed to a minimal operation he called Merge, which consists basically of joining different elements (be they words or phrases) iteratively in a binary tree that is able to generate all syntactic structures (Chomsky 1981). It is interesting to note that in the opinion of the evolutionary linguist Derek Bickerton, Merge may more accurately represent the brain mechanisms involved in language than does recursion, as it refers to the binding and connectivity of lexical items in terms of their semantic significance (Bickerton 1990, 2009, 2014). Furthermore, Bickerton boldly asserted that by creating Merge, Chomsky "assassinated" his own child, recursion. He went on to argue that all recursive structures can be achieved solely by using Merge, with no need for recursion. Thus, it is the lexical properties of words that determine the binding rules and the resulting hierarchies of phrase structure. In Bickerton's view, what is critical for the initial emergence of language is not syntactic structure but a lexicon and its associated semantic representation. He said that this of course is only the basics. Much more is needed to develop modern language, including grammatical elements of inflection, case marking, etc. that are not accounted for by this model.

Chomsky's perspective has been also criticized by linguists like Steven Pinker and Ray Jackendoff, who argued that phonology also shows a unique syntactic organization (but different from phrase structure) and highlighted the relevance of many other aspects of language, including semantics, the lexicon and large-level discourse structure (Pinker 1994; Jackendoff 1999). Pinker and Jackendoff claimed that syntax is actually a mechanism to represent hierarchical cognitive mechanisms in a phonological dimension. In particular, Steve Pinker advocated a more biologically based perspective on language. In line with Charles

Darwin, he saw language evolution as a highly complex adaptive process at all levels, from the remodeling of peripheral vocal structure to the elaboration of instinctive learning mechanisms, very much like the acquisition of birdsong or the development of flight in birds. According to Pinker, language is in fact unique, but so are the elephant's trunk and many other specialized organs in the animal kingdom.

Shared or Unique?

Considering the above, it is not surprising that in relation to language evolution, Chomsky has always been skeptical. In his early years Chomsky claimed that the complexity of language was such that it was impossible to find an organization so intricate in general cognition, even less in animal communication. Furthermore, his view that language is perfect does not admit the possibility of a gradual acquisition of distinct elements. It is either complete, or it is not. However, in later years, coincident with his strategy of simplifying his syntactical theory, Chomsky has become closer to biology and evolutionary theory. He teamed up with evolutionary psychologist Marc Hauser, who up to that point had strongly advocated a gradual Darwinian evolution of language. After what was probably very intense conversations at the beginning of this century, Chomsky and Hauser reached an agreement in which they parceled the study of language into two territories: one amenable to comparative and evolutionary studies (Hauser's domain) and the other reflecting the core elements of language and impenetrable to evolutionary analyses (Chomsky's domain). In 2002, they published a now highly cited paper, together with co-author Tecumseh Fitch, whom we met above, in which they made a clear distinction between what they termed the faculty for language in the broad sense (FLB, Hauser and Fitch's expertise), and the faculty for language in the narrow sense (FLN, Chomsky's expertise) (Hauser et al. 2002). FLB includes all biological traits shared with other species or with non-linguistic cognitive mechanisms, while FLN is a single monolithic and