

I. FONDEMENTS

CONSIDERATIONS ON THE EMERGENCE OF HUMAN LANGUAGE

Alexandru GAFTON,
„Al. I. Cuza” University of Iași
algafton@gmail.com

Abstract

Like other animals, man expresses his simple and acute states by sonorous and imagistic manners that are more expressive than words, but these acts have too little to do with superior mental faculties. Many animals possess vocal organs with the same general structure, which they use to communicate, so it is possible they should develop in the same direction. Several other animals have vocal organs, but they do not use them too well to communicate, which is related to the level of development of their brain and intelligence. But what differentiates man from the other superior animals is not the mere articulation, the understanding of uttered sounds or even the simple ability to assign certain sounds to certain ideas. It is man's infinite ability to associate the most various sounds to various ideas, which comes from the great development of the human mental ability.

Keywords

Language, communication, learning, anatomic structure, social bases

Preliminaries

As every language needs to be learned, it goes without saying that human language is not an instinct or a deliberate invention. And since man has a tendency to speak, language is not an art either. It is a slowly, gradually and unconsciously developed subproduct of the biosocial evolution of a primate.

In this context, imitation plays an important part in acquiring (i.e. learning and producing) the uttered language, originating in the imitation and alteration of various natural sounds, from the voice of other animals to one's own sounds produced and accompanied by gestures. After this first step in

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the formation of vocal-articulated language, as voice was used more and more for this purpose, the vocal organs oriented and perfected in this direction, based on the transmission of the effects of use, which worked towards the development of the ability to speak. Furthermore, the ties between the active and frequent use of language and the development of the brain became close, so that at the appearance of the genus *Homo*, man's ancestor must have been much more evolved than the other primates. The continuous exercise of these abilities influenced the mind, activating it in a new direction and stimulating it to function towards the development of thinking, so that a complex thought can no longer be produced in the absence of the word. Thus, the uninterrupted use of language worked on the brain and produced transgenerationally transmissible effects, which affected the ameliorative development of speech, coevolution of language and thinking, leading to structural and functional changes that were later transmitted transgenerationally¹.

Natural sounds

Given certain physical conditions – the most important of which is the presence of an (atmospheric or aquatic) environment in which atoms can move freely – and biological ones as well – the most significant being the anatomic endowment of animals with elements such as an air sac at the end of a system of tubes (or with organs that can rub against each other), and due to the ability to develop certain somewhat expressible affective and emotional states and to interact, the animals came to produce perceptible sounds. The capacity to react responsively and act imitatively to environment-generated stimuli and the mere natural exercise of the various organs producing inherent and natural sounds brought about the emission of sounds from the fundamental category of those produced by a fruit falling from a tree or by grass being stomped by a predator. After the spontaneous and semiconscious emission of sounds carrying purely natural information, the exercise in that direction could lead to the production of sounds with communicative potential. Following the relatively intense and contextualized production,

¹ Darwin 1875.

evolution and selection of sounds, some of them acquired vital meanings (the identification of the source of food, danger and potential advantages or disadvantages). The animals with such an anatomy which had learnt this use of sounds became apt to use that source for a different purpose than the initial one, as a result of a process of exaptation or using the elements of a spandrel in such a manner.

Exaptation is a process of reorientation – not exclusive – of a role of a constitutive part in order to perform a different function from the initial one, together with which that particular structure has possibly developed. Adaptation refers to the situation in which the organism responds to certain adaptative (internal and/or external needs) using its abilities and creates adapted means for survival in certain conditions. Exaptation refers to the situation in which the organism adds new functions to the same structure – possibly by operating small adaptative restructuring².

Spandrel is a metaphorical term borrowed from architecture designating a secondary – unnecessary and unharmed – product, a result of evolution by adaptation and natural selection, which is a phenotypic trait. This result may be particularly useful to evolution because it may serve adaptation or it may turn into a useful tool of survival and reproduction³.

Although animals can produce sounds in various ways and manners, generally for anatomical and physiological reasons, with most of these animals it is the sounds generated by the upper airways that predominate. It is thus proven that vocalisation is a natural and current ability, related to the anatomo-physiological complexity of certain components of those particular beings.

Speech

The transition from isolated or interlinked sounds that human organism can produce to their formation as elements of a communication system allows one to observe the fact that human (vocal-articulated) speech shares features with other similar systems (mainly avian) and the

²Gould & Vrba 1998; Norde & van de Velde 2016.

³Gould & Lewontin 1979; Solé & Valverde, 2006.

acts and developments it implies rely on perception, subsequent memorisation, production of vocal imitations, learning and adaptative-ameliorative evolution.

The premises of the appearance of human language

A hotly debated issue, the emergence of the vocal-articulated human speech has not yet rid itself of stakes and prejudices and research has not yet been able to provide overwhelming evidence to support a hypothesis or a correct set of hypotheses. This is probably due not so much to the still insufficient level of investigations as to the complexity of the issue.

This almost inextricably combines the need to find the biological and social premises which made it possible for certain biological developments to acquire usages and develop needs that should generate a tool and a way of social communication. Those developments must have been quite strong and important at the species level which supports the idea of polygenesis of human language. The latter must have relatively simultaneously developed within several communities, isolated from each other, starting with the stage in which the development of the human being and of the community required and allowed this. Moreover, it is difficult to admit that the initial development was unhindered, continuous and successful, meaning that neither the human being, perhaps, nor definitely the current vocal-articulated language are the results of a first constitution that prevailed and continued to this day. It is very likely that, in various areas, different developments should have occurred, functioning to some extent and later disappearing, sometimes leaving traces behind, i.e. they were not continuous. Then, because biosocial factors and needs went on working imperiously, the developments re-emerged and maybe some of them gave in again until a time in which they started to become stable, to acquire a necessary nature and to generalise within the species⁴.

Usually, when the effort is made to find out how the initial process of the emergence of human vocal-articulated language occurred, most researchers consider the occurrence of developments that led to anatomic

⁴Dor 2015.

evolutions (the appearance or mutation of genes, appearance or modification of neural structures and of anatomico-physiological structures, in general) and functional ones (the development of social behaviours in a coevolutionary way, possibly as response to a new necessity). Being in a position to indicate things more precisely, some researchers make choices in one direction (structural) or another (functional), generally taking into account an adaptive process, and tend to hierarchise the previously outlined complex of causes. Thus, some tip the balance in favour of the FOXP2 gene, of bipedalism or of the mirror neurons⁵, for example, pointing out that the evolutive origin of human language lies in the basal anatomical substrate, lateralised to the left hemisphere⁶.

Following the functional exercise and development of the structure, the organism came to access and, at the same time, to alter larger, deeper and more complex areas of its interactional environment (physical, biological social). The complexity of these newly emerged demands challenged the functional structures beyond certain thresholds of complexification, the evolutive solution thus arising being to acquire a way of making energy consumption more efficient and its products more profitable. This solution is lateralisation, a form of structural and functional asymmetry. Thus, the liver or the heart have asymmetrical positions, whereas structures such as the hands or the legs, though symmetrical, are asymmetrical in terms of the individual's inclinations and, consequently, in terms of their abilities (attack, defence, feeding, cleaning etc. are not carried out equally by using any hand and the apparent symmetry of swimming and walking is the result of a pressure towards symmetry not of actual symmetry)⁷.

Similarly, in the brain, lateralisation occurs structurally (starting with less clear aspects, such as the external configuration of the whole, going through some already more obvious ones and reaching the networks of neural and sanguineous circuits) and functionally (various processes and actions such as vocal articulated speech, writing, the numerous control and

⁵Kohler *et al.* 2002; Galati *et al.* 2008.

⁶Gannon *et al.* 1998.

⁷Corballis 2017b.

regulations processes etc.). In contrast with what it may look like at first glance, the brain is not a ‘mirror’ organ.

As regards the left cerebral cortical lateralisation, which is the topic of this paper, it is present in both chimpanzee species (*Pan troglodytes* and *P. paniscus*) as well as in other animals, therefore it is not an exclusively human trait⁸.

Others believe that human language is the consequence of living within a community and of the need for social cohesion⁹, which prompted the transmission of information in the form of stories¹⁰ or gossip¹¹, or that the transition from gesture to voice occurred by means of music¹². They also say that language is the product of love¹³ (seen not as an emotion, sentiment etc., as in the current and common understanding at the profane, scientific, psychological, philosophical, theological etc. level, but as complex biosocial state and process)¹⁴, resulting from the mother-offspring interaction¹⁵, for love is also related to socio-cultural causes and to the biological development in the environment, at the same time acknowledging the crucial nature of the plasticity of the brain¹⁶.

Finally, according to some others, language development derives neither from the biological organism nor from the language of the environment, but from the functioning of perceptual systems, which detect the relationships between language and the world, using them to orient attention and action¹⁷, whereas others believe that the emergence of language is due to the dynamic structure of the social-interactive environment in which the child evolves¹⁸.

⁸Gannon *et al.* 1998.

⁹Dunbar 1996; 2012; 2017; Falk 2004; 2009; Sheridan 2005.

¹⁰Dor 2015; Dunbar 2017; Boyd 2005.

¹¹Dunbar 1996; Dor 2015.

¹²Dunbar 2017; Killin 2017.

¹³Burunat 2015.

¹⁴Burunat 2014; 2016.

¹⁵Falk 2004; 2009; Sheridan 2005.

¹⁶Burunat 2015.

¹⁷Dent 1990.

¹⁸Zukow 1990.

Although they seem to be in contradiction, endowed only with their own reasons, all these opinions, some of which very refined and considering fine elements of detail, are connected to the bases of human language and none can be categorically denied at a certain level, all of them being acceptable from a certain perspective and for a certain stage of the process. This is because human language is not the consequence of a single factor or of a biological or/and social occurrence, but the result of a multitude of factors and events, some derived from others, all intertwined at a given moment and having deep and entangled, evident or latent roots. Such evolutions issue from the co-occurrence of several states and processes, which have become effects and factors, interlinking and potentiating each other, generating cascade and convergent effects, at least partially, i.e. not unidirectional effects, but often developed and acting on several levels and concurring only in some of their sometimes-secondary aspects. Therefore, the only fact that cannot be accepted is the absolutizing of a cause or a factor, with the implicit elimination of all the others.

Since its inception, language must have been the early result of the complex manifestation of several factors, having several causes and acting under several pressures. As it was exercised, the development it underwent was sequential, with various outcomes (including those in the category of causes and factors) producing new causes, factors and effects, always entwined and generating new ways of existence and patterns of action, always growing into a coevolutionary spiral. At the different moments of its formation, functioning, dissemination, development, consolidation and becoming, it is but natural that one or the other of the aspects highlighted by the various researchers should have had some importance in accordance with the requirements of the stage. The result at various times, however, could have been generated only by the entire complex of causes and factors, under the entire complex of pressures that, during the process of complexification, prompted ones to grow, others to be born, all of them stimulating, modelling, modifying and nurturing the development of the complicated behaviour and secondary biosocial product, to different extents, though.

The extent to which each of these hypotheses can be demonstrated and its compatibility with the vocal-articulated language as organ and tool, as gradually and historically developed structure and behaviour, make one probably believe that: a) the foundation of language is material and motor¹⁹; b) it does not emerge as a consequence of a revolution that caused the appearance of ‘something’ ‘new’, but rather as a result of a development that could be structurally and behaviourally speculated, which generated a diversification in both respects. In fact, as one will further see, researching the relationship between gesture and vocal language – at motor and neural levels – may lead to understanding that mental activities appear and develop as a result of the interactions between the biological organism and the natural and social environment²⁰.

Organic premises. The examination of the matter on a phylogenetic scale reveals that the initial roles and functions of organs which form the complex known as the *phonation apparatus* were connected to fundamental vital processes (nutrition, breathing, perception etc.). The particular evolution of a certain branch of hominids comprised several modifications, from genetic to structural ones²¹, then neural and behavioural. These elements’ interrelating, exercising together and later coevolving, along with the resulting functional changes, could entail the unification of those components and the adaptation of the whole resulting complex, in a direction that was to allow some kind of behaviour and some kind of use of them (communication by means of vocal-articulated sounds). Naturally, the exaptation process occurred slowly, without abandoning the initial roles and functions, with partial outcomes and with the relative concord of the structural and functional states. The current result was gradually reached at the cost of gruelling efforts, required by subsequent needs, which entailed consistent anatomophysiological modifications. Considering only the articulating anatomophysiological structures or the neural ones, or the very human language, one notes that they are so complex because their evolution must have occurred

¹⁹Savage-Rumbaugh *et al.* 1993; Ferretti & Adornetti 2014.

²⁰Iverson & Thelen 1999.

²¹Lieberman *et al.* 1972; Fitch & Giedd 1999.

gradually, over a period of time that goes beyond the origins of modern man, 2-3 million years ago²².

FOXP2 is a gene from several regions of the brain and is present in its own and characteristic forms in the genetic endowment of many other animals, having numerous roles in the development of animals in which it exists. The amino acid sequence and the pattern of neural expression of FoxP2 genes are extremely well-preserved, from reptiles to humans, which points to the important role this type of genes plays within the vertebrates' brain – regardless of the presence or absence of any relationship with vocal imitative learning. At the same time, its expression indicates the neural zones and circuits which have had a crucial role in the developments and evolutions that brought language into existence and in the development of those particular neural circuits and the behaviours they mediate²³.

In humans, the changes occurring in various areas of the brain – connected by the basal ganglia circuits that are related to the FOXP2 gene – along with the mutation of this gene (most likely subject to evolutive pressures and the target of natural selection)²⁴ favoured the appearance of speech (without the abandonment of gestures)²⁵. As several data types point out, the FOXP2 is involved in language²⁶, but is not a gene of 'language'. This is not only because there are genes which have a unique and exclusive role²⁷, but also because it is involved in brain development – being essential for modulating the plasticity of important neural circuits²⁸ – and in the functioning of certain specific areas (with effects on language, speech and knowledge), then in the development of lungs and of the oesophagus, as well

²²Harrison 1995.

²³Scharff & Haesler 2005.

²⁴Enard *et al.* 2002.

²⁵Gentilucci & Corballis 2006; Gentilucci *et al.* 2008; Reimers-Kipping *et al.* 2011; Schreiweis *et al.* 2014.

²⁶Maricic *et al.* 2013.

²⁷Jablonka & Lamb 2005.

²⁸Fisher & Scharff 2009.

as in the control of the expression of other genes²⁹, its presence making it more difficult for breast cancer to appear³⁰.

In mice, FOXP2 affects motor coordination, the learning of ultrasonic vocalisations, the development of lungs, brain and oesophagus, being also involved in brain modelling, bone remodelling, the consolidation of upper limb and intervertebral disc strength, i.e. in the development and morphogenesis of some components, which, in humans, contributed to the appearance of speech. Its absence in mice entails serious (potentially lethal) lung developmental defects and failure of oesophageal muscular development, as FOXP1 and FOXP2 are the most important regulators of lung and oesophagus development, the entire family of FOX genes cooperating within the tissues in which its members are co-expressed³¹.

FOXP2 is involved in the formation of neural circuits regulating motor and cognitive abilities³². Through the entire complex of actions and effect its functioning brings about, this gene has led to the coevolution of anatomic and neural adaptations related to speech and bipedalism and is deeply involved in the appearance and stabilisation of speech³³. It is also engaged in the acceleration of the probabilistic acquisition of language features by means of the segmentation of language and action elements, facilitating the transition from declarative to procedural learning, thus adapting the brain to human language³⁴.

Crucial for the vocal learning, this gene, which is indispensable to speech and language acquisition, is involved in other forms of motor learning as well, so that, as far as it is known today, this gene type (in the forms present in different species) seems to play a key role within the neural circuits in charge of motor learning. Therefore, the structural alterations of the gene,

²⁹Vargha-Khadem *et al.* 1998; 2005; Lai *et al.* 2001; 2003 Enard 2002; 2011; Teramitsu *et al.* 2004; Groszer *et al.* 2008; 2009; Fisher & Scharff 2009; Kurt *et al.* 2009; Gaub *et al.* 2010; Watkins 2011; Dediu 2015; Staes *et al.* 2017; Murphy 2018.

³⁰Cuiffo *et al.* 2014.

³¹Shu *et al.* 2007.

³²Lieberman 2007.

³³Xu *et al.* 2018.

³⁴Schreiweis *et al.* 2014.

performed in the vinegar fly, affect the brain anatomy and motor learning and habit acquisition processes (equivalent to those governing vocal and linguistic learning in humans)³⁵. In fact, the importance of this gene for human language was discovered following the attempt to ascertain the causes of some deficiencies with linguistic consequences in a family³⁶.

Basal ganglia. The appearance and development of basal ganglia was a neural change important for the emergence of language³⁷, playing a significant part in language acquisition and learning³⁸. These agglomerations of neural bodies, gathered in a relatively well-delimited structural assemblage of grey matter, located at the base of cerebral hemispheres, are essential for higher cognitive functions, among which the strengthening of learning and procedural memory, and for the emotional behaviour (their damage may affect the cognitive function and emotional behaviour). Although the major role of basal ganglia refers to motor control, given that their function goes beyond motor planning and control and governs the initiation, amplification and refinement of signals facilitating decision making, they are important for controlling vocalisation³⁹. In terms of our discussion, their chief role, during childhood, is to train the patterns of the motor vocal tract; during adulthood, they are involved in the emotional-prosodic modulation of utterances⁴⁰.

Various experts, who have made experiments and observations, present different conclusions in many respects, but the data so far – extracted from the analysis of the role and involvement of basal ganglia – are likely to provide a general conclusion on the relation between structures and functions, confirming the opinions claiming that motor systems have had a significant role to play in the appearance of higher cognitive functions⁴¹.

³⁵ Mendoza *et al.* 2014.

³⁶ Vargha-Khadem *et al.* 1998; 2005; Lai *et al.* 2001; Watkins *et al.* 2002.

³⁷ Vargha-Khadem *et al.* 1998; Brainard & Doupe 2000a; Scharff & Haesler 2005; Bolhuis *et al.* 2010; Enard 2011; Simonyan *et al.* 2011; Watkins 2011; Kojima *et al.* 2018.

³⁸ Ackermann *et al.* 2018.

³⁹ Booth *et al.* 2007.

⁴⁰ Butler & Hodos 2005; Nieuwenhuys *et al.* 2008.

⁴¹ Lieberman 2007; Zenon & Olivier 2014.

The physiological basis necessary for the sensorimotor skills required by articulated speech was provided by the morphological changes initiated by the FOXP2 gene in the basal ganglia⁴². This contributed to the fine regulation of the cortical circuits of the basal ganglia, which is relevant for the acquisition and plasticity of the language of birds and humans⁴³. The connections with the cerebellum (which is engaged in certain cognitive functions, in acts of articulation, segmentation of the sonorous flow and control of coarticulation and which includes circuits that build and store internal representations of the linguistically generated world on the long term) enable the basal ganglia to participate in language production and processing⁴⁴, being involved in auditory retroversion, sensorimotor adaptation and learning⁴⁵. Through their relations with other brain nervous structures and due to circuit loops, basal ganglia acquire the potential to transmit information and thus, by means of the developed connections, to take part in purpose-driven behaviours⁴⁶.

Vocal tract movements led to movements that created syllabic and metrical patterns – an important step in verbal sensorimotor acquisition. The role of basal ganglia in the process of accommodation of laryngeal and supralaryngeal movements involved in articulation, in that of processing the signals related to evaluation and selection and in motor learning has been crucial. They have helped exercise and the results of exercise get established on certain coordinates, whereas the patterns of motor speech have become automatised.

As many other complex motor skills, speech is not innate either. It appeared during evolution and was acquired gradually, through the trial/error process. Studies conducted on birds – which learn how to produce complex vocalisations by means of trial and error – show that the learning process involves actions with exploratory and evaluation variability of the resulting

⁴²Flaherty & Graybiel 1994; Lieberman 2007.

⁴³Brainard & Doupe 2000a; Enard 2011.

⁴⁴Desmond & Fiez 1998; Macoir *et al.* 2013; Nozaradan *et al.* 2017.

⁴⁵Houde & Jordan 1998; Bohsali & Crosson 2016.

⁴⁶Miyachi 2009.

performances, with a view to acquiring motor skills leading to the improvement of the performances of this faculty. Given the relationship between basal ganglia and rapid behavioural variation – related to vocal learning⁴⁷– and between emotive prosody and the amount of dopamine⁴⁸, it is clear that basal ganglia played a major part within the new type of communication behaviour.

Bipedalism. Throughout evolution, during the occurrence of evolutive acquisitions, morpho-structural changes, which are difficult to explain in terms of the causes that induced and determined their occurrence, happened relatively often at anatomical level. However, they brought about a cascade of events, intertwined and potentiating each other, by themselves and by their consequences⁴⁹. One of these changes was the hominines' standing on their hind limbs, probably a sporadic to frequent occurrence, which offered benefits and was selected evolutionarily and, in the case of *H. sapiens sapiens* – at an ontogenetical level and from a certain age – became the only (or the dominant) way of terrestrial locomotion and a premise for other changes⁵⁰. This positional change became permanent and entailed skeletal, cerebral, circulatory, respiratory and digestive modifications, developments, adaptations and evolutions, virtually affecting all the organs, apparatuses and functions of the organism as well as the relationships among them, with various and sometimes interlinked consequences – a process that led to the modification of the type of control over breathing⁵¹ and an increase in the accuracy of sounds produced⁵². Naturally, the biological, behavioural, social, mentality etc. developments, adaptations and evolutions do not occur due to the action of only one factor and much less of an event, which implies that none of these evolutions are exclusively the result of bipedalism. Even so, the biped stance was the one that triggered and supported those evolutions, exercising pressures which caused a wide range of modifications. Such a

⁴⁷Kojima *et al.* 2018.

⁴⁸Simonyan *et al.* 2011.

⁴⁹Vaughan 2003; Friedman 2006; Harcourt-Smith 2007; Corbalis 2009; Hurford 2014.

⁵⁰Harcourt-Smith 2007.

⁵¹MacLarnon & Hewit 1999.

⁵²Savage-Rumbaugh *et al.* 1993.

change could have been the deep and major cause of the morphological change, three of the consequences of bipedalism being of particular interest here: a) the increase in volume of the skull and brain; b) the descent of the larynx and c) the release of the forelimbs.

Increase in volume of the skull and brain. Bipedalism resulted in a number of structural changes which brought about adaptative-evolutive modifications of the ontogenetic patterns in the brain, a process which led to its morphological reorganisation and diversification. The evolutive reorganisation of the development occurred in three major ways: a) the modification of prenatal development of the cranial base and of the face – which reflects the adaptation to bipedalism; b) an increase in the growth rate of the skull in the first period after birth – an essential process to get a bigger brain; c) the specific change in facial development – which reflects dietary adaptations⁵³.

The evolutionist alteration of the cranial ontogenetic programme led to the morphological reorganisation of the skull and its diversification – because evolution favours the situation in which several (or slightly differentiated) solutions appear within a path, and if they are viable and possibly useful, they have chances of survival. Although nature has found means of making energy consumption more efficient, given that there is no direct, univocal and absolutely mandatory relationship between the size of structures and functional complexity, one may say that the size of the human brain has played an important role in the establishment of human higher skills.

The brain is a computational organ par excellence (i.e. rational in an etymological sense). Its calculations consider the survival and reproduction of the organism which has developed it and which it serves⁵⁴, hence all its possibilities and concrete ways of existence and functioning in an efficient manner. Through the brain, the body acquires the ability to perceive similarities and differences, to classify, compose and decompose information, to draw conclusions and, based on these, to actuate the organs⁵⁵.

⁵³Bookstein *et al.*, 2003; Zollikofer 2012.

⁵⁴Martin 1983; Givón 2002a; Jablonka & Lamb 2005.

⁵⁵Martin 1983; Givón 2002a; Jablonka & Lamb 2005.

The increase in brain size is due to environmental and dietary factors⁵⁶, social factors⁵⁷, modifications and developments of sensory channels⁵⁸; more competitive senses and increased skills need a more efficient ‘manager’ which, once a certain evolutive threshold has been exceeded, implies a bigger organ. Although the process of growth of the brain size is simultaneous with the appearance and evolution of modern mammals, it is not necessarily associated with an increase in intelligence or in the intellectual skill. The increase in brain complexity objectively entails modifications of the volume and automatically includes structural modifications with functional consequences. In this respect, the number and nature of synapses are more important than, say, those of individual neurons.

Vocal communication – including that of other mammals and birds – is in coevolutive relationship with the brain and requires a brain capable of determining and processing the vocalisations of a particular species. Therefore, the ability to speak involved morphological causes at the base of the skull (compartmentalisation of components, relative positions, volume, their relations).

Descent of the larynx⁵⁹. The structures which experienced adaptations, exaptation and functional developments, acquiring roles in vocalisation – such as the larynx or the mandible – also underwent evolutions with structural results which would later be used to form a phonation apparatus.

Humans’ great acquisition, which the other primates lack, was the structural-functional complex that could bring about the ability to produce vocal-articulated speech, resulting from the stabilisation of evolutions and adaptations with certain genetic, morphological (neuromuscular and bone) and functional structures, used in hundreds and thousands of small functions and coordinates in order to generate an inventory of sounds upon which speech rests.

⁵⁶Bailey & Geary 2009; de Casien *et al.* 2017.

⁵⁷Bailey & Geary 2009.

⁵⁸Leakey & Lewin 1992.

⁵⁹Crelin 1987; Lieberman *et al.* 2001.

Both structurally and functionally, the larynx shows traces of the successive adaptative modifications to the environment and life conditions, the coevolution of morphology and activity leading to morphological adaptations that developed the function which, in its turn, encouraged the evolution of the structure for the purpose of exaptation. Thus, the larynx – a sphincter protecting the lungs of certain aquatic creatures – became an organ capable of allowing a high intake of air and, in a certain creature, a speech organ⁶⁰.

Although the laryngeal descent is not an exclusively human feature, as it is also encountered in other mammals and primates (in chimpanzees, for instance, it is primarily caused by the descent of the laryngeal skeleton relative to the hyoid, but it is not accompanied by the descent of the hyoid relative to the palatal plane), in human adults, whose larynx is descended in the neck, it is the result of an adaptative response to demands unrelated to vocalisation itself, but from which it has benefited⁶¹. The positional changes of the larynx must have occurred at least partially during the hominid evolution – not all of a sudden – and involved functions such as breathing, swallowing, locomotion and vocalisation as well as some evolutive changes of these mechanisms, along with a change in the relationship between phonation and articulation for the purpose of vocalisation. The process has two stages: a) the laryngeal skeleton descends relative to the hyoid – phylogenetically, in the ancestors of humans and chimpanzees, ontogenetically, in children – and b) the hyoid descends relative to the mandible and cranial base, in humans⁶².

The results of research conducted on chimpanzees (males and females), aged between one month and 14 years, focusing on the changes in size and shape of the pharynx, the vocal tract, the spatial positions of the larynx, hyoid, mandible and hard palate, relative to one another and to the oral cavity, as well as on growth lines point out that certain aspects regarding the vocal tract shape have obviously changed in ontogeny, primarily in the

⁶⁰Hast 1983; Negus 1929; 1949

⁶¹Fitch & Reby 2001.

⁶²Marshall 1989.

first year and before adolescence. The ratio between the pharynx height and the oral cavity length (important in speech) decreases with age and stabilises.

The larynx and pharynx in the first hominids were probably located in the upper part of the neck, as they are in present-day primates (excluding man). Such a position would allow breathing and a good placement of the epiglottis, necessary for food ingestion, without endangering the airways, but would hinder the ability to change laryngeal sounds⁶³. The position of upper respiratory structures (larynx and pharynx) is important for understanding breathing, swallowing and the ability to vocalise. On the other hand, the shape of the basicranium and its exocranial orientation are related to the positioning of laryngeal and pharyngeal structures, which is in relation to the upper respiratory system, because there is a close connection between the degree of basicranial flexion and the position of upper respiratory structures due to the established mechanical relationships between the cranial base and the area linked to it, which contribute to the act of breathing⁶⁴.

In children under the age of 1 and other primate species, the relationship between the alterations of the basicranial line and the changes in the upper respiratory system is similar; the upper respiratory structures are in an elevated position, the tongue entirely in the oral cavity and the epiglottis easily covers the glottis.

In human new-borns, there are various structural and functional differences as compared to the adults⁶⁵. Thus, the location of structures and the opposition of the glottis relative to the palate allow the infant to breathe and suckle, stimulating nasal respiration. The positioning of structures is adapted and is different from that of the adult (the larynx is in a more vertical position, the thyroid cartilage is in and under the hyoid arch, vocal cords are rather transversal, the epiglottis is short etc.). The child's larynx differs from that of the adult in terms of consistency, size, position and shape. With the exception of the hyoid – a bone that, in adults, has been identical in size and shape to the current one for the last at least 60,000 years, which shows that it

⁶³Laitman & Heimbuch 1982.

⁶⁴Laitman & Reidenberg 1988.

⁶⁵Prakash & Johnny 2015.

is very unlikely for changes to have occurred in the visceral skeleton since then⁶⁶—, the structure is cartilaginous and apparently amorphous, the airway is narrow and the larynx is located in the upper part of the neck.

Although at birth the hyoid and the larynx are higher than in other mammals, they descend gradually, then the process continues at an accelerated rate in the first part of childhood, after which the laryngeal skeleton descends relative to the hyoid and so does the hyoid relative to the mandible and the cranial base. After the second year of life, exocranial flexion between the hard palate and the foramen magnum occurs in humans, a change which coincides with others happening at the level of positional relations within the upper respiratory system. At the same time, the tongue and larynx descend in the neck, altering their functional relations. There is a tight relationship between the exocranial orientation at the base of the skull and the positioning of upper respiratory structures as well as between the larynx position, the orientation of pharyngeal constrictor muscles and the orientation of the occipital base⁶⁷.

That is why the human larynx is large, the partially pharyngeal tongue separates the epiglottis from the palate (the decreased contact between the epiglottis and the palate is obvious in many primates, but in these, the pharynx is small, the tongue is oral, thin and long), the human supralaryngeal vocal tract develops into a double resonant system that is just as long horizontally as it is vertically. From an acoustic-articulatory perspective, such a morphology of the phonation apparatus, the location of the pharynx relative to the basicranium, breathing⁶⁸ along with the tongue mobility contribute to the appearance and development of the articulated speech process and to the production of complex sounds.

At the species level, the larynx is not differentiated and displays similarities and structural correspondences in various animals⁶⁹. Able to resonate and emit sounds as a result of several types of events

⁶⁶Arensburg *et al.* 1989.

⁶⁷Laitman *et al.* 1978.

⁶⁸Laitman & Reidenberg 1988.

⁶⁹Hast 1983.

(communication is implicit, the difference carrying or being able to carry meaning), the larynx has come to be defined by the innervation system rather than by the morphology and interrelations of components. The physical foundation of phonation is the laryngeal skeleton – including the vocal cords.

The first phase may be associated with the evolutionary changes in swallowing. The descent of the hyoid and of the larynx relative to the mandible is caused by the functioning of the muscle involved in deglutition and points to the various functional roles of the hyoid during speech (it provides the basis for the movements of the tongue participating in vocal tract articulations, as speech requires the independent control of these functions) and transport of the food bolus. This process increases the risk of accidental choking during swallowing, reduced risk of early acquisition of the movement (ascent of the hyoid, compatibility of the laryngeal skeleton with the hyoid, bending of the epiglottis and obstruction of the laryngeal orifice). It is remarkable that the process occurs although the spatial constraints related to deglutition impose greater restrictions on the rate and degree of orolaryngeal descent than the adaptations required by vocalisation.

A development of the swallowing mechanism, adapted to dietary changes and to the consistent growth of the hominid organism, the first descent weakens the link between the laryngeal skeleton and the hyoid, allows the epiglottis to lose contact with the velum and the larynx to move independently of the hyoid and shows that these physical connections were weak in the ancestors of chimpanzees and humans⁷⁰.

The mere fact that, at the birth of the human being, part of the equipment is not positioned and prepared to produce speech does not indicate some kind of economy (as in the case of the lungs devoid of air, for example) but points out that speech was a recent acquisition, which had not yet passed from ontogenesis to phylogenesis. It is an acquisition which is not necessary for the mere survival of the creature, a potential that can be updated not only by simple exercise – as many others –, but by prior structural and morphological changes.

⁷⁰Lieberman *et al.* 2001.

The second descent increased the risk of accidental aspiration of fluids and food and may be connected to the skeletal developments evolving in the hominid period, namely the ventral cranial base flexion during childhood, reduced prognathism due to sphenoid shortening and increased mandibular size. Along with tongue mobility, these modifications of the facial and mandibular skeleton contribute to the appearance of the double resonator⁷¹.

Release of forelimbs. The transition to the bipedal stance was a slow process, which probably occurred accidentally and sporadically at first; then it was adopted in certain situations for which it was suitable and efficient and was gradually assumed completely entailing the loss of adaptations peculiar to the four-legged posture. Furthermore, this stance brought about infinitely more than its primary and direct benefits. Used sporadically or systematically, the bipedal stance allowed the release of the forelimbs resulting in their being used for purposes other than support and locomotion. The new usages proved to be profitable, both by extending the range of possible actions and by acquiring new attributes of these very uses, which created the premise for conjugating the instinctive and deliberate or controlled adoption of the bipedal stance. Thus, the succession of operations led to their amplification, following the path from diversification to refinement.

In algebraic and geometric proportion, such a development starts by using hands to perform actions for which other parts of the body were used (adaptation), then fulfilling new activities – impossible or never done before – (exaptation) and comes to operations performed at unprecedented quality levels (improvement)⁷². Thus, due to the occurrence of a phenomenon followed by morphological and structural changes and by ensuing functionalities and as a result of the coevolution of structure, function, use and demands, a structure which probably served for swimming, support and terrestrial movement, for grip, defence and attack becomes one which can do all this and many other things (calligraphic writing, painting, playing musical instruments, various artistical or technical operations of infinite finesse) with increasingly improved accuracy and delicacy.

⁷¹Nishimura *et al.* 2003.

⁷²Corballis 2009.

But the release of the forelimbs is important in this discussion because bipedalism opened the way to the production of manual gestures and also allowed one to look at the other one's front of the body – and implicitly at the other one's face –, which led to exploiting and enhancing body movements, in general, and orofacial ones, in particular.

Gesture. To a greater extent than sounds, gestures are a natural given. Considering this as well as certain anatomic (structural and nervous) and functional determinations, the onset of communication is probably related to symptom and natural gesture⁷³– which are natural acts also capable of taking on relevance and significance. At the same time, gestures are important, even indispensable, for the process of learning how to make tools, in which case they may prevail over speech, especially during the stage when the apprentice is inexperienced. Then, under verbal guidance, the production of tools becomes more efficient, gesture and word develop one another and extend the entire complex of activities through the network they thus form, coevolving at the same time⁷⁴. Thus, the making of tools is closely related to communication⁷⁵.

By the manner in which it appears and develop and by the gradual amplifications of its effects, gesture is phylogenetically and ontogenetically important⁷⁶ and has social implications and consequences⁷⁷, generally participating in the cumulative cultural evolution and contributing to its progress⁷⁸. The symptomatic nature of gestures⁷⁹, therefore, makes them implicit and then suitable for being used in interindividual communication (from a producer to a certain receiver), as gesture underlies the articulatory act⁸⁰.

⁷³Thelen 1979; Poizner *et al.* 1987; Browman & Goldstein 1989; Blake *et al.* 1992; Blake & Dolgoy 1993; Kimura 1993; Armstrong *et al.* 1995.

⁷⁴Morgan *et al.* 2015.

⁷⁵Frey 2008; Jablonka *et al.* 2012; Steele *et al.* 2012; Stout & Chaminade 2012; Cataldo *et al.* 2018.

⁷⁶Hewes 1973; Bates *et al.* 1989; O'Neill *et al.* 2005; Gentilucci & Corballis 2006; Goldin-Meadow *et al.* 2007; Corballis 2009; Kelly *et al.* 2010; Jablonka *et al.* 2012; Sterelny 2012; Corballis 2013; Goldin-Meadow & Alibali 2013; Esteve-Gibert & Prieto 2014; Hurford 2014; Dewaele *et al.* 2015; Boundy *et al.* 2016; Kendon 2016; Corballis 2017;

⁷⁷Smith & Delgado 2013.

⁷⁸Jablonka *et al.* 2012; Sterelny 2016.

⁷⁹Fónagy 1988.

⁸⁰Studdert-Kennedy & Goldstein 2003.

Although they can communicate – and, based on this, may serve for communication – orofacial gestures are limitative because they fulfil their role only if individuals are close enough to one another (or to others) and maintain a good eye contact. In their turn, brachial gestures may become complementary, thus opening the circle. As long as the community is not too big (several dozens of individuals), the relationship between its needs and communication skills can be harmonious and such a solution works. The increase in interactions within large groups⁸¹ makes gesture – which is not as nuanced and liberating as speech – no longer be able to satisfy those needs adequately.

The fact that gesture can be used as an articulatory movement⁸² probably facilitated the appearance and adoption of ‘speech’, which responded to the growth of: a) the community, b) the frequency and intensity of contacts within it, c) the need for precision in communication. However, the association of speech with the communication system existing until then enhanced the force of communication and diversified its possibilities – naturally, with increased need to master the system well. This process occurred naturally, as a consequence of an evolution probably determined by the manner in which the organism formed, because brachial manual, orofacial and orolaryngeal movements are controlled by structures located in Broca’s area (F5 area in the other primates), where there are also some of the mechanisms relating perception to action⁸³.

Therefore, given the plasticity of organs and of body mechanisms, in general, the relative directed and intense exercise of the organs involved in vocalisation and articulation would entail the formation of motor and nervous networks which were to serve speech and gradually specialise – without this process of exaptation leading to the elimination of other fundamental or derived functions of the components of that particular complex.

The aforementioned reveal another important aspect of this discussion, namely the plurimodal nature of the brain. Thus, some impulses

⁸¹Cataldo *et al.* 2018.

⁸²Meneill 1992; 2012.

⁸³Heiser *et al.* 2003; Binkofski & Buccino 2004; Arbib 2005a; Skipper *et al.* 2007; Petkov *et al.* 2009.

the brain transmits entail – in children – movements of hands and prattling⁸⁴. Like the brain, communication – even in its elaborate form, the vocal-articulated speech – is also plurimodal⁸⁵ (plurimodality is no stranger to other primates⁸⁶). This kind of communication is supported by the development of certain areas of the brain (particularly the parietal ones) and by their relationship with one another⁸⁷.

Mirror neurons. A natural extension of the action of recognition and a central factor for culture, mimetic capacity⁸⁸ is involved in the unfolding and evolution of countless processes of organismal and social development and evolution, its evolution serving as basis for becoming a necessary precursor of language.

Due to a neural pattern from the premotor areas (generated by observing the action and similar to that generated by the occurrence of the action), primates have a fundamental mechanism of recognising the action performed by others. Following the acquired observation, the mere perception or just the thought in that direction may stimulate the energetic discharge towards that part, which triggers an adequate response to the behaviour observed or mentally evoked. This process occurs by means of the mirror neurons and indicates the close relationship between the representation of reality and speech. Observation – from the actor to the observer and vice versa – of the fact that an involuntary response affects behaviour leads to recognising or assigning an intention and to establishing a dialogue; this is the core of language. The mechanism of mirror neurons is fundamental to empathy, understanding and imitation, and, in humans, to learning and language as well⁸⁹.

Broca's area has a mechanism which activates the neurons when visual stimuli provide perceptions of an action which, once observed, may trigger the performance of that action. In other primates, the corresponding

⁸⁴Petitto & Matenette 1991; Petitto *et al.* 2001.

⁸⁵Slocombe *et al.* 2011; Sterelny 2012; Levinson & Holler 2014.

⁸⁶Tagliatalata *et al.* 2007; 2011; Meguerditchian *et al.* 2014

⁸⁷Murphy 2018.

⁸⁸Buccino *et al.* 2004; 2004a; Maran 2011.

⁸⁹Rizzolatti & Craighero 2004; Iacoboni & Dapretto 2006; Levy 2011; Chirilă 2019.

area (F5 area) coordinates the muscular movements of the upper limbs, in relation to a visual or auditive stimulus (audio-visual mirror neurons), whereas in humans it is the centre which controls articulatory movements in relation to an auditive stimulus⁹⁰.

If in the orofacial communication system the addition of a sound could only enhance the meaning of facial expression (the performance precision being not too important), the moment sounds acquire descriptive value they are bound to remain identical with themselves, in identical situations, and to clearly differentiate, in different situations. In other words, in order for the gestural communication system to function, it is not strictly necessary for imitation to be rigorous. An approximate or quite inaccurate communication can be satisfied by appropriate tools and has the advantage that it can be practised by anybody. A communication whose needs for precision increase requires the exact imitation of sounds – the development of vocal-articulated speech being the very solution meeting such a demand. It is thus understood that all elements and factors engaged in the process undergo evolutions and coevolve in relation to the imperative nature of the need.

Primates are animals which tend to perform by imitation what they have perceived by senses; to them, the actions of others (mainly those of their fellow creatures, but not only) represent stimuli and are potential models, sometimes of vital importance. The very social organisation is impossible without considering these sequenced and hierarchised stimuli. At the same time, even if the elements of the act, their enchainment, the entire act have taken shape in the mind (although it is hard to prove that the mind is not wrong), the muscular, nervous etc. components need activation and exercise in order to get results similar to mental projections, i.e. the executive organs need exercise, which is carried out by various classes of stimuli.

The tendency to communicate using any means and investing energy is typical of primates. Thus, chimpanzees can construct means of auditive communication for specific purposes, generating a system through which they communicate efficiently⁹¹, whereas orangutans, which produce sounds using

⁹⁰Fogassi & Ferrari 2005.

⁹¹Hopkins *et al.* 2007.

a tool, in order to signal something modulated⁹², are able to select the tactics that remedy failed communications, depending on how well they are understood; in case of partial understanding, they repeat these signals and if there is no understanding, they change the way of communication⁹³.

Being a natural extension of the action of recognition and a central factor for culture, mimetic capacity⁹⁴ is thus engaged in the evolution of so many processes of organismal and social development, underlying a necessary precursor of language.

Broca's area has a mechanism triggering the neurons when visual stimuli provide perceptions of an action which, once observed, may cause the performance of that action. In other primates, the corresponding area (F5 area) coordinates the muscular movements of the upper limbs, in relation to a visual or auditive stimulus (audio-visual mirror neurons), whereas in humans it is the centre which controls articulatory movements in relation to an auditive stimulus⁹⁵.

Coupled with the mechanisms of learning, the generic structures which accord action with its performance set off the cultural evolution of human languages. Transcending and enclosing orofacial and brachial manual communication, the vocal-articulated language appeared gradually as a result of the evolution of a basic mechanism which originally was not related to communication: the ability to recognise actions⁹⁶. Without being a human feature, the gestural-manual system exploited the system of matching observation with performance and paved the way for the evolution of the open vocalisation system, known as *speech*⁹⁷.

⁹²Hardus *et al.* 2009.

⁹³Cartmill & Byrne 2007; Leavens 2007.

⁹⁴Buccino *et al.* 2004; 2004a; Maran 2011.

⁹⁵Fogassi & Ferrari 2005.

⁹⁶Meltzoff & Moore 1977; 1983; Gallese *et al.* 1996; Stamenov & Gallese 2002; Ferrari *et al.* 2003; Buccino *et al.* 2004; 2004a; Leslie *et al.* 2004; Arbib 2005; 2012; Skipper *et al.* 2007; Arbib *et al.* 2008; Molenberghs *et al.* 2009; Whitehead 2010; Fogassi & Ferrari 2012; Gentilucci *et al.* 2012; Petit 2012; Repetto 2012; Braadbaart *et al.* 2014; Mooney 2014; Fogassi 2017.

⁹⁷Heiser *et al.* 2003; Iacoboni, 2005; Gentilucci & Bernardis 2007; Abramson *et al.* 2018.

The semi-abandonment of communication through signs and the exercise in the new direction required the use of complex sound emissions (combinatorial sounds), and the new anatomic potential made language move from its brachial manual origins to the emission of sounds. Gradually, gestures would lessen their importance, vocalisation would gain autonomy and thus the relationship changed, for gesture became an accessory (however, instinctually, it did not disappear, as it remained a companion reflecting the genesis of the entire functional structure – as certain reflexes or movements remain associated with each other). As a consequence of these updated possibilities, the speech lateral circuit developed, this neural premise underlying interindividual communication and eventually the vocal-articulated language⁹⁸.

Social premises of human language. At the confluence of behaviour and development there may occur a multitude of capacities, finely conjugated as the creature acts and interacts in a given environment and at a given moment⁹⁹. After the emergence of a functional structure, correlated with other parts of the whole in which it participates, the development by exercise of this structure and, at the same time, the correlation of structure and function with others stimulate or at least provide the premises for the complexification and refinement of that structure and of its functions.

Sociality and cooperation. Primates' biological endowments, lifestyle, exercising and adaptative evolution led to the development of their own behavioural patterns. The ability to combine objects, to build and use tools and do all this in increasingly complex manners is common to many primates, for the same neural circuits and areas govern the combination of

⁹⁸Lieberman *et al.* 1972; Bruner 1975; Holloway 1981; Tomasello *et al.* 1985; Kurata & Tanji 1986; Tobias 1987; Petitto & Marenette 1991; Kendon 1994; 2014; Rizzolatti *et al.* 1996; Goldin-Meadow 1998; Blake 2000; Butcher & Goldin-Meadow 2000; Corballis 2003; Petitto *et al.* 2004; Arbib 2005a; Ozçalışkan & Goldin-Meadow 2005; Gentilucci & Corballis 2006; Armstrong & Wilcox 2007; Capirci *et al.* 2007; Goldin-Meadow 2007; Roy & Arbib 2007; Gentilucci & Dalla Volta 2008; Gentilucci *et al.*, 2008; Villarreal *et al.* 2008; Aboitiz & Garcíá 2009; Corballis 2009; 2010; Tellier 2009; Smith 2010; Aboitiz 2012; Cartmill *et al.* 2012; Gentilucci *et al.* 2012; Liebal & Call 2012; Macedonia & Kriegstein 2012; Braadbart *et al.* 2014; Bohn *et al.* 2016; Goldin-Meadow 2017; 2018; Tramacere & Moore 2018.

⁹⁹Iverson 2010; Evans 2014.

symbols and the use of tools, the performances achieved by the other primates matching those of two-year-old children¹⁰⁰.

More than in the other primates, due to the increasingly demanding development through exercise, to their endowments and performances, humans came to distinguish themselves in terms of the connection between the various emotions they experienced, creation and use of tools, subsequent cortical differentiations, acquiring distinct, relatively modular skills necessary for the complex combination of objects and for grammar.

An important aspect is domestication, a phenomenon which spread and expanded. Thus, the contact with a domesticated fellow creature influenced and amplified one's own domestic state, on the one hand, and stimulated the conversion of competitive situations to collaboration¹⁰¹ (for example, the common upbringing of children¹⁰²) and their harmonious mixture (as in the case of real emulation), on the other hand. These acquisitions tended to be used for the establishment of subsequent functions, which were complexified and in accordance with those advanced stages¹⁰³. The secondary results of the domestication process and the entailed coevolution provided complex bases for the communication process (in general), including the abilities to acquire the vocal one, i.e. of vocal-articulate language¹⁰⁴.

Within this social framework of competitive collaboration, vocal-articulated language came to facilitate all human activities, stimulating their development in certain directions. Hence, one may conclude that when it appeared, language must have been part of the computational network¹⁰⁵—which might account for its tendencies to dominate the other behaviours.

The fact the actions and behaviours contributed to an overwhelming extent to the emergence of such complex functions is also proved by the

¹⁰⁰Greenfield 1991.

¹⁰¹Nowak & Krakauer 1999; Corballis 2009; Tomasello 2009.

¹⁰²Jablonka *et al.* 2012; Dor 2015.

¹⁰³Theofanopoulou *et al.* 2017; Murphy 2018.

¹⁰⁴Calvin 1982; Davidson & Noble 1993; Gibson & Ingold 1993; Jablonka *et al.* 2012; Stout & Chaminade 2012; Aboitiz 2017; Marquez 2017; Theofanopoulou *et al.* 2017; Murphy 2018; 2019.

¹⁰⁵Morgan *et al.* 2015.

anatomy of the brain, viewed in relation to language. The Broca and Wernicke areas, constitutive neural circuits and the connections between areas involved in language in general, the situation of other primates point out that language was nothing but a consequence of some evolutive developments of cerebral and nervous structures, arising from the exercise oriented by special needs. (The other primates have remarkable skills, which cannot be minimalised, to engage in symbolic and nuanced communication¹⁰⁶). Furthermore, the fact that lateralisation might be related to the differentiated distribution of spatial and sequential abilities – in that the making of tools would lead to a lateralised tendency to the left side in order to perform sequential movements, which proved useful for language – reinforces the abovementioned because lateralisation implied the specialisation of two types of memory systems, active memory for sequential (and possibly identification) tasks on the left side, active memory for tasks related to spatialisation on the right side. This shows that lateralisation is not the result of the specialisation of cerebral areas, but of the organisation of those particular neural networks, with the left hemisphere strengthening the connections with the frontal lobe and the right one with the areas involved in sight. (Hence, the slight differences in anatomical organisation between the left and right areas involved in language.)¹⁰⁷.

All this supports the assumption that such a complex behaviour as language is rooted in the intertwining and coevolution of a biological organism equipped with various possibilities of development and subject to certain demands required by its enhanced exercise, in a stimulating environment, which led to the development and amplification of those possibilities that, in an increasingly challenging environment, were able to fit into a coevolutive spiral.

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¹⁰⁶Savage-Rumbaugh *et al.* 1986.

¹⁰⁷Aboitiz & García 1997.

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