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AN UPDATED EVOLUTIONARY RESEARCH PROGRAMME FOR THE CO-EVOLUTION OF LANGUAGE AND CUMULATIVE CULTURE

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...but it is very striking that there isn't just one way of modeling the world, there are often two ways of modeling the same phenomenon and depending of what kind of mind you have you may find one or the other illuminating.

John Maynard Smith

ABSTRACT

The aim and the structure of this work are twofold: a general analysis of the current status of the evolutionary research programme will serve as a general framework for an inquiry in specific aspects of a much debated field-study: the evolution of language. This case-study will do as a sort of testing arena to put at work the explanatory tools of the evolutionary research programme, in order to show what conceptual framework can better deal with the unsolved issues associated to the chosen case-study. Hence this work will be characterized by a continuous interplay between specific issues pertaining to the level of evolutionary biology (evolutionary processes at work, morphological, behavioral and cognitive adaptations) and theoretical analysis pertaining to the meta-level of philosophy of science (like conceptual and terminological analysis, causation mechanisms in play, research programmes' evolution).

In the Preface we try to delimit the scope of this work, as the chosen case-study is characterized by a strong interdisciplinarity. In the Introduction we provide an essential historical reconstruction of the language evolution debate, starting from Darwin and Wallace's times, identifying some key concepts that will serve to navigate the contemporary debate. We then move forward identifying the common structure of some language evolution hypotheses that have been proposed across the years and highlight some limitations. We also discuss the necessity of providing a proper definition of the language faculty in order to display the evolutionary inquiry accordingly; we take into account the FLB – FLN distinction and highlight some limitations as well. In particular we show the difficulty by the Standard Evolutionary Theory (SET) conceptual framework in integrating the cultural dimension in language evolutionary explanations. We then stress the importance and the necessity of operating such an integration and we argue that the Extended Evolutionary Synthesis (EES) conceptual framework provides an explanatory toolkit that is better equipped to solve such a task. We then present an abstract model (the assimilate-stretch principle) that is able to provide in principle this integration, exploiting some of the key concepts of the EES conceptual framework. We then show that a co-evolutionary model between language and cumulative culture might be a promising path to integrate biological and cultural evolutionary processes, trying to rely our argument on results from co-evolutionary comparative studies (the cultural drive hypothesis).

The three central chapters of this work consist of independent papers that were written at different stages. Each one of them deepens a specific aspect but all three of them share the common intent to show how the EES conceptual framework can be properly put at use.

The first chapter is dedicated to an exploration of the Self-domestication hypothesis in human evolution through the analysis of a selection of critical examples concerning genus *Homo* evolution,

relevant for the evolution of language, such as the evolution of hominin life-history traits, the enlargement of the social group, increased cooperation among individuals, behavioral change and innovations (the use of fire), heterochronic modifications leading to increased synaptic plasticity. It is argued that a relaxation of selective pressures caused by niche construction activity might have played a role both in human and language evolution.

In the second chapter, the selected critical examples presented in chapter one are explicitly analyzed through the lenses of the EES conceptual framework. The evolution of language is treated as an open problem in the evolutionary research programme and it is shown how four factors (niche construction, inclusive inheritance, phenotypic plasticity, developmental bias) and two concepts (reciprocal causation, constructive development) can be usefully exploited to gain a better understanding of human and language evolution.

The third chapter explores a specific theoretical issue linked to the EES debate, that is the need to revisit the distinction between proximate and ultimate causes of evolution. In fact, cultural transmission, operating at an intermediate level between the ontogenetic and the phylogenetic one, can be assumed to be both a proximate and an ultimate mechanism, with associated different predictions. We argue that assuming one or the other position leads to two different perspectives of how biological and cultural evolution interact. We argue in favor of an *integrative* perspective, that is acknowledging culture as an ultimate cause, in agreement with an EES-inclined conceptual framework. We also discuss the consequences of this theoretical shift and show how this can shed light on the evolutionary rate of language evolution (punctuationism and gradualism) debate.

In the Conclusions we advance some further proposals, two in particular: first, we treat language as a form of teaching, specifically verbal teaching, and re-examine the hypothesis, presented in the previous chapters, that language could have evolved as a form of high-fidelity transmission mechanism; second, we discuss the proposal according to which language can be intended as a major transition in evolution and in particular we propose to split this transition in two steps: the first concerns the evolution of cumulative cultural capacities, the second the evolution of language; these two steps could share a common evolutionary process at their bases and we suggest this could be identified in an expanded version of the assimilate-stretch principle, which we propose in the conclusions, discussing also possible future directions.

Finally, we conclude that gene-culture co-evolutionary models are proving their fruitfulness not only to shed light on human evolution, but also on other social species, and that the EES conceptual framework provides a set of explanatory tools that results appropriate to deal with these issues.

PREFACE

Research in language evolution represents one of the most intriguing and at the same time challenging field of study in science. The nature of this research is strongly and necessarily interdisciplinary, as it puts together elements from anthropology, archeology, linguistics, historical linguistics, neurobiology, cognitive psychology, evolutionary biology, genetics, artificial intelligence, game theory, philosophy and complex systems research. Each of these domains is essential for language evolution inquiry, making it one of the "hardest problems in science" (Christiansen and Kirby, 2003).

Obviously, no single researcher can cover such a wide range of expertise, so some choices have to be made in order to face such a complex matter. This work is primarily a work of philosophy of biology. Philosophy of biology is a particular branch of philosophy of science and it must be conceived as a philosophy of particular science, dealing mainly with 4 kinds of issues (see Pievani, 2015b):

1) the specificity of biology compared to other sciences (Mayr, 2005)
2) what kind of inferences characterize scientific explanation (and evolutionary explanation) in biology (Pievani, 2013)
3) conceptual and terminological analysis of fundamental objects of biological inquiry (gene, species, information, evolution, etc.; see for example Stotz and Griffiths, 2011)
4) how scientific research programmes evolve in biological fields (Pievani, 2011; 2015).

It is a common tendency in philosophy of science today to specialize in particular scientific subfields, in order to deal with specific problems of the discipline instead of trying to apply a rather generalist analysis based on logical argumentation. Ernst Mayr (2005) argued that a healthy philosophy of biology should develop in the direction of a philosophy of particular science. The work proposed here will develop in particular the fourth point of the list just proposed.

Scientific research activity takes place within cultural and historical spans characterized by sets of ideas, conceptual tendencies and theoretical assumptions underlying the scientific practice. Evolutionary biology found its grounding conceptual framework during the first half of the XX century with the Modern Synthesis, namely the unification of Mendelian genetics and population-level Darwinian evolutionary theory. This incredible work was initiated by the combined effort of eminent statistician Ronald Fisher, poliedric scientist J. B. S. Haldane and geneticist Sewall Wright, and brought forward by other evolutionary biologists like Julian Huxley, Theodosius Dobzhanksy, George Gaylord Simpson, Ernst Mayr Mayr, 1982), among the other eminent scientists. The result was a fruitful research programme able to explain adaptation and diversification of living beings. Some assumptions were put at the core of the Modern Synthesis:

1) the pre-eminence of natural selection as the major driving and creative force in the evolutionary process
2) a gene-centric perspective, assigning to genes a causal primacy over phenotypic variation, regarding genetic inheritance as the only inheritance system. The criterion chosen to define an evolutionary process was *change in gene frequencies across generations*: selection, mutation, drift and gene flow were regarded as *evolutionary processes.*
(3) evolution is always a gradual accumulation of small and randomly arisen genetic variants
(4) macroevolution can be derived from microevolution.

This set of core assumptions guaranteed the long success of evolutionary biology, intended as the genetic theory of natural selection, for the whole XX century. However, some themes of research were neglected, or at least they were not given a central role in the architecture of the Synthesis: in particular development and ecology.

According to Mayr's (1961) distinction between proximate and ultimate causes in biology, development falls within the proximate mechanisms, consequently it plays no active role in the evolutionary process, which instead is characterized as a historical explanation of differential survival of organisms and their genes. However, researches accumulated in the second half of the XX century showed the interconnections between evolution and development (Gould, 1977) and today this study culminated in the Evo-Devo research programme (see Moczek *et al.*, 2015). Moreover, the understanding of the interactions between organisms and their environment was further inquired in the second half of the XX century: studies on phenotyipic plasticity (West-Eberhard, 2003) and on the ecological niche (Odling Smee *et al.*, 2003) showed a more interactionist and constructive perspective, overcoming the idea of a unidirectional causality flowing from the selective environment to the organisms.

Today a debate is open on the need to update the evolutionary theory along these themes (Laland *et al.*, 2014; Laland *et al.*, 2015): on one side there are the defenders of the Standard Evolutionary Theory (SET), on the other side the supporters of the Extended Evolutionary Synthesis (EES).

Laland *et al.* (2015) provide a comparison of the main core assumptions at the heart of these two conceptual frameworks (see Table 1).

Table 1. A comparison between SET and EES core assumptions (see Laland et al., 2015).

SET core assumptions	**EES core assumptions**
Pre-eminence of natural selection	Reciprocal causation
Pre-eminence of genetic inheritance	Inclusive inheritance
Random genetic variation	Non-random phenotypic variation
Gradualism	Variable rates of change
Gene-centred perspective	Organism-centred perspective
Macroevolution from microevolution	Macroevolution not by microevolution alone

The EES approach shows some fundamental theoretical shifts, compared to the SET core assumptions, that can be summarized in some keywords: niche construction, inclusive inheritance, phenotypic plasticity, developmental bias, reciprocal causation, constructive development (Laland *et al.*, 2015).

According to the EES supporters, causation in biology is fundamentally reciprocal: variation in one element modifies another element to which it is causally linked and this modification eventually feeds back its consequences to the starting element. *Niche construction* (Odling Smee *et* al., 2003) is a typical example of this feedback model of causation: variation in the organismal activity brings variation in the ecological niche in which the organism operates and the modified environment generates novel selective pressures that modify organism's evolution across generations. The interaction between organisms and their environment is seen from a constructive viewpoint from the EES perspective. Genetic inheritance is considered only one of the multiple systems of inheritance that contribute to phenotypic variation across generations: epigenetic inheritance, ecological inheritance, behavioral or cultural inheritance and parental effects are other independent but interacting systems of inheritance; genes are not the only type of information that is transmitted across generations from this *inclusive* perspective. *Phenotypic plasticity* plays a fundamental and underestimated role in evolution: organisms can exploit their plasticity to flexibly adjust to environmental variation without any alterations in allele frequencies across generations; if selective pressures stay consistent enough, genetic fixation of the advantageous (and randomly emerged) variants will eventually follow; this perspective was labeled genetic assimilation or genes-as-followers, as in this case evolution is not driven by mere genetic variation, but rather genetic variation is a result of a plastic adjustment to novel environmental conditions. Moreover, not only organismal activity (niche construction) can systematically bias selective pressures, but also *developmental constraints* can bias the possible solutions that natural selection can explore.

The EES research programme relies on some core assumptions summarized in Table 1. However, we think that some of them are more arguable than others (see Pievani, 2015a). For example, posing the focal level of the evolutionary inquiry only on the organism (organism-centred perspective) might miss some fundamental hierarchical interactions between levels (top-down and bottom-up causation; see Okasha, 2011); moreover, we think the assumption that macroevolution is decoupled from microevolutionary needs more theoretical refinement in the EES inclined researches today present in literature.

Laland *et al.* (2015), beyond assessing what the core assumptions of the EES research programme are, claim the existence of a structure and of a set of predictions. We believe that the EES implant is still far from being organized in a coherent and consistent structure and more theoretical work is much needed from this viewpoint. Moreover, according to an evolutionary epistemology perspective in which two scientific theories compete for providing the best explanations, strictly speaking, a research programme represents an expansion of its rival research programme only when it is able to show that its predictions are able to explain new facts that the rival research programme is not able to explain, relying on different and novel assumptions compared to the rival research programme (Motterlini, 2000). The EES research programme still has to prove that it is able to produce a consistent set of predictions that set it apart from SET conceptual framework: the next years will be crucial for this enterprise, and this crucial point will establish the nature of the epistemological evolution we are witnessing today in evolutionary sciences. The debate is open and alive.

In this work, we will try to show how this general debate on the epistemological status of the evolutionary research programme finds a testing arena in a much debated field study, full of unsolved issues: the evolution of language. In particular, we will stress that, according to the analysis proposed here, in order to face these issues, it is indispensable for the evolutionary research programme to make a major integration, that is incorporating the interactions between classical biological (or genetic) evolution and cultural evolution. The evolution of language is hence treated here as a case-study to tackle this issue: how to integrate biological and cultural evolution in an updated evolutionary research programme. The explanation we will propose here consists of a co-evolution between transmission mechanisms and culture during the long course of human evolution. We will show how all the key epistemic elements of a EES are indispensable ingredients for a gene-culture co-evolutionary explanation. We argue that this in principle represents an expansion of the scope of the evolutionary research programme.

This work has been conceived in the form of 'paper collection'. Each paper was written as an independent work; however, the three papers, each of which represents a chapter, explore a specific part of a larger whole. In this sense, the Introduction serves as a wide common denominator to frame the complex topics inquired in this work. A summary of the main key points associated to the debate on language evolution will be given in the Introduction, to allow who is not familiar with this topic to share the crucial concepts. Among the many facets of this debate, the Introduction will serve also to take a specific direction that will be developed in the three chapters and in the conclusions. The latter will give some suggestions also on how the issues treated here can be further inquired in the future.

INTRODUCTION

1. A long debate: from Darwin to Chomsky

Language has always represented a thorny issue for evolutionists, since Darwin and Wallace times, diverging in interpreting the role of natural selection in shaping human intelligence and language capacities. The co-discoverer of the principle of natural selection Alfred Russell Wallace (1823 – 1913) argued that human intellectual faculties (the brain, consciousness and language) could not be the product of the action of natural selection, provoking Darwin's discourage and disappointment when the support of his colleague was most needed (Wallace, 1869, 1870). Famous *Wallace's argument* was based on the observation of the so called primitive populations, possessing a brain as big as the one possessed by the civilized white man, but with apparently alleged inferior mental faculties. If brain size would be the product of natural selection acting on adaptive and functional mental faculties, primitive and civilized brain sizes should significantly differ, due to the alleged different mental capacities. As natural selection cannot foresee the future and build structures that are not serving a specific use, Wallace argued that the human brain, and the associated mental faculties, could not have evolved for the effect of natural selection, but rather some other "superior" force should be responsible for such an accretion. According to Wallace, a qualitative difference stands between humans and the rest of the animal reign: humans crossed a Rubicon that no other species ever crossed.

More than a hundred years after this fundamental debate, influent linguist Noam Chomsky (1988) still defended a rather similar *discontinuist* and *qualitative* viewpoint on language evolution (Parravicini and Pievani, 2016) assessing that natural selection could not explain why humans are provided with a complex computationally powerful cognitive device which has no equals in other animal communication systems: Universal Grammar (UG). In its early formulations, UG is conceived as an innate, biologically grounded and genetically determined faculty, which provides the predisposition to acquire language to all members of *Homo sapiens* species. According to UG supporters, this shared computational cognitive device leads children to learn languages within some constraints features: the result is that languages across the world show fundamental shared grammatical features called language universals (Croft, 1990; Hawkins, 1998).

Language universals were first identified by American linguist Joseph Greenberg (1915 – 2001) comparing approximately thirty languages across the world. A simple example of spoken language universals are vowels and consonants; also, all languages are provided with nouns and verbs, but it is less clear whether all languages display subjects and objects. Linguists proposed different hypotheses for such alleged shared features of world languages: monogenesis (all language derive from an ancestral language possessing these features); language contact (communication among individuals and population brought world languages to "hybridize" and to share common features); functional explanation (it is functional for languages to have these features, in terms of learnability, commuincation efficiency, etc.); innateness. The latter hypothesis spread in the linguists community as the most plausible during the so called Cognitivist Revolution in the second half of the XX century, led by Noam Chomsky. In strong opposition to Skinner's Behaviorism, according to which the child's mind at birth is a *tabula rasa*, an empty box (or an unfathomable black box) which gets filled with learning stimuli (and consequently language is acquired through trial and errors and reinforcement), Chomsky argued that a language acquisition device pre-existed the external stimuli through which languages are acquired after birth. The multiplicity of stimuli a child's mind has to cope with are too many, too various and not language-specific to let the child acquire language properties in a remarkable short amount of time ("poverty of the stimulus" argument). According to Chomsky, the innate component allows to select the relevant stimuli and build languages within some constraints determined by this innate, biological, cognitive toolkit, that was named Universal Grammar. Through the second half of the XX century, UG passed from being conceived as a complex interplay between mental/cognitive modules, to a single computational mechanism defined Merge (Minilmalist Thesis), embodying the core recursive properties of syntax (property of embedding linguistic elements in one-another; property of generating hierarchical linguistic structures; property of discrete infinity, that is making infinite use of finite means).

Although conceived as a biologically grounded trait, UG sudden emergence during human evolution is not considered by Chomsky to be consistent with Darwinian gradualism and evolutionary continuity.

"it seems rather pointless (…) to speculate about the evolution of human language from simpler systems—perhaps as absurd as it would be to speculate about the "evolution" of atoms from clouds of elementary particles" (Chomsky 1968: 61).

Chomsky's account of language emergence was a nonfunctional one. The abstract properties of UG did not relate to communicative or pragmatic considerations. Indeed, it has been argued that many aspects of UG may even hinder communication (e.g., Chomsky, 2005), further highlighting the nonfunctional nature of UG.

Chomsky stresses in particular that language should be conceptualized not as a social practice, but rather as the output of an organ or module hard-wired in the human brain: language is *in primis* a tool for thought rather than a means of communication that could be shaped by social selection.

Influenced by the theoretical framework of the Cognitivism that intended to remark the distance from Behaviorism, Chomskian account assigns primacy to Internal-Language (I-L) as a cognitive, computational device and conversely assigns an almost negligible role to External-Language (E-L), that is the geographically contingent realization of the universally shared biological core. This stance is sometimes labeled (Neo)Cartesianism for recalling a similar form of Dualism (separation) between mind and the outer world (Ferretti, 2010).

This stance assigns to language an (1) irreducible complexity that is believed to be not the product of the slow and gradual action of natural selection (*saltationism*: *de novo* and abrupt emergence of a full-developed complex organ) and (2) a qualitative difference from any other animal communication system, a difference in kind and not in degree (evolutionary *discontinuity*).

These arguments against the usefulness of natural selection in explaining language evolution are quite similar to the critiques that British zoologist George Mivart moved against Darwin's theory of Natural Selection and its gradualist explanation for the evolution of complex adapted traits (Mivart, 1871). According to Mivart, the gradual action of natural selection cannot explain why the 5% of a complex trait such as a wing or an eye should spread within the population, as it would serve no use at all. In the 60s and the 70s of the XIX century other scholars such as Max Müller, a famous German philologist, supported an anti-Darwinian explanation of language evolution, embracing this discontinuist perspective.

Darwin's reply to Mivart's critiques are contained in the last edition of the *Origins of species* (Darwin, 1872), introducing the principle of what Gould and Vrba (1982) would have labeled later *exaptation*: the current function of a trait can be decoupled from its historical origin. A trait might have served a certain function or might have emerged as a structural by-product of some developmental effect (*spandrel*, see Gould and Lewontin, 1979) and might have been coopted or *exapted* for a new function only in a secondary phase, following some reshaping of the ecological niche and of the associated selective pressures. Hence, a 5% of a complex organ might have served a different function before being coopted for the current function (type 1 exaptation). Brids wings, for example, were probably exploited for thermoregulation before being coopted for flight. A structural by-product of some developmental effect, serving no specific functions, tolerated by natural selection, might be coopted for a new function once the ecological conditions require it (type 2 exaptation). A typical example is the so called “panda's thumb”, a hypertrophic wrist bone (sesamoid bone) exploited by the animal (belonging to Ursidae family, hence a former carnivorous that changed its diet) to grasp bamboo while eating it (on the different types of exaptation see Serrelli and Pievani, 2011).

Chomsky's stance regarding the relationship between human language and evolution changed several times across the years and it is quite difficult to recognize a coherent and continuous position (see for example Hauser *et al.*, 2002). Today, UG in the so called "Minimalist program" (Chomsky, 1993) is equated to Merge, the capacity that embodies the central recursive property of syntax (a key component of the language faculty) to compute linguistic information hierarchically. Merge allows to embed linguistic elements such as phonemes in words (phonology) and words in meaningful sentences (syntax); this operation has the property of "discrete infinity", as a finite number of elements can produce a potentially unlimited number of new combinations. In this sense UG is intended in a modularist framework (Fodor, 1983) as a cognitive domain-specific device dedicated to language acquisition and production.

Recently the eminent linguist endorsed what he describes as a evo-devo perspective on language evolution, arguing in favor of a rather lucky (and however still unobserved to date) genetic mutation providing Cognitively Modern Humans (CMHs) with a structural modification (and still nonfunctional) that allowed the emergence of the full-developed language capacity approximately 100 – 50 kya (Chomsky, 2010; 2012; Berwick and Chomsky, 2016). However, the probability of randomly building a fully functioning, and completely novel, biological system by chance is infinitesimally small (Christiansen and Chater, 2008). Today this "lucky mutation" or "magic bullet" hypothesis on language evolution, making a complex trait emerging abruptly, is considered almost anti-darwinian in literature (Hillert, 2015) and so incompatible both with the known action of evolutionary processes and with the definition of the language faculty (which will be discussed later on).

The reason we quickly summarized these key points here was to put in light some fundamental conceptual elements that can help in providing a general framework for the language evolution debate. Here we propose a categorization:

1) *the function-selection problem*: is language the outcome of the action of continuative selective pressures on a specific function, such as communication (*adaptation*), or did it evolve as a non selected by-product from structures previously involved in other tasks (*exaptation*)?
2) *the evolutionary rate problem*: did language appear abruptly in human evolution (*saltationism*) or was it the outcome of a long, step by step, uniform cumulative evolutionary process (*gradualism*)?
3) *the comparative problem*: is the language faculty uniquely possessed by humans (*autapomorphy*), representing a qualitative difference from other animal communication systems (evolutionary *discontinuity*) or is it, or are some of its subcomponents, traceable in other non-human animals (*synapomorphies*), being an example of evolutionary *continuity*?

4) *the protolangiage problem*: which, if any, kind of language (*protolanguage*) was possessed by the hominin ancestors of modern *Homo sapiens*?
5) *the ethological problem*: in which measure language is biologically determined (*innate*) and in which measure is it culturally determined (*acquired*)?
6) *the multilevel problem*: regarding the evolutionary processes that acted on language, have they acted at the *individual* level or have they acted at the *population* level?

We believe that this categorization provides a set of helpful conceptual tools that will help navigate the main aspects of the debate on language evolution.

2. Internal Language and a Naïve evolutionist view

In 1990, MIT psychologists Stephen Pinker and Paul Bloom tried to reconcile Chomskian definition of language with evolutionary biology, providing an adaptationist hypothesis for UG, still intended as the species-specific trait that distinguishes human language (Pinker and Bloom, 1990). Their argument goes as follows: according to Darwinian evolutionary theory, the only natural process able to shape complex, domain-specific, adapted traits is natural selection and human language is exactly a complex trait that should be intended as the product of natural selection. Language has been selected by the slow action of continuous selective pressures for a specific function conferring fitness to its bearers. As the eye (a complex organ) was slowly shaped by natural selection for visual functions, so was language for communicative functions. Even though Pinker and Bloom could have challenged Chomskian assumption about E-L irrelevance at its roots, they were cautious in stating the specific function language was selected for. However, communicative efficiency was retained the most plausible candidate, as current language shows efficient design for communication.

From this follows that functional communicative systems of lower efficiency were probably present before modern language, that is protolanguages: pidgin and creols are considered living examples of the plausibility of the existence of such lower-efficiency communicative systems (Bickerton, 1990).

Although Pinker and Bloom's work has the merit of “naturalizing” the study of language evolution, the problems associated to a discontinuist (hence an anti-darwinian) view are not totally overcome. In fact, what they were trying to naturalize was Chomskian UG, that is a biological, cognitive device that has no equal in the animal kingdom, that is believed to be uniquely human, and is thought to be not derivable from other animal communicative or cognitive traits (Pinker, 1994).

Considering UG as an adaptation, which means a *de novo* emerged and optimalized trait, suffers exactly this kind of problems. Continuity is hard to meet if language is equated to UG, intended as a genetically determined cognitive leap, separating humans from other non-human animals.

Pinker and Bloom hypothesis however argues against a saltationist account and in favour of a gradual evolution of language, in accordance with Darwinian theory. However, the detalis of this gradualism are not exposed properly. The two authors instead simply assume that every small variation in grammatical competence must have conferred selective advantage to its bearer, lasting long enough to be fixed in the ancestral population. They explicitly refer to genetic variation:

> "For universal grammar to have evolved by Darwinian natural selection, it is not enough that it be useful in some general sense. There must have been genetic variation among individuals in their grammatical competence. There must have been a series of steps leading from no language at all to language as we now find it, each step small enough to have been produced by a random mutation or recombination, and each intermediate grammar useful to its possessor" (Pinker and Bloom, 1994, p. 36)

Pinker and Bloom do not deny the eventuality that cultural dynamics may have played a role in the evolution of the human capacity for language and they explicitly discuss the possibility of gene-culture co-evolutionary dynamics (Hinton and Nowlan, 1987), discussing the plausibility of interactions between learning and innate structure resulting in a Baldwin effect (Baldwin, 1896; Simpson, 1973). However, they also highlight that:

> "the ability to use a natural language belongs more to the study of human biology than human culture; it is a topic like echolocation in bats or stereopsis in monkeys, not like writing or the wheel" (Pinker and Bloom, 1990, p. 708)

By stressing this, a marginal evolutionary role is expressively attributed to culture.

The tentative reconciliation of human language with the evolutionary theory proposed by Pinker and Bloom is affected by the adoption of a rather simplistic view of evolution, that Tecumseh Fitch labeled the *naïve evolutionist* view (Fitch, 2012). This view can be summarized in some fundamental points:

1) *a prime mover logic*: the evolution of language wants to be explained by finding those genetic mutations that are believed to be the necessary and sufficient conditions for the emergence of

language. Genes cause the phenotype and genetic variation always precedes phenotypic variation.
2) *unidirectional causality*: genes are believed to be the prime mover for language evolution (unidirectional causal arrow from genes to the phenotype) and selective pressures acting over genetic variance is considered the only ultimate cause for language evolution (unidirectional causal arrow from the selective environment to the genetic variance).
3) *atomistic approach*: language is equated with a single trait, a single component, that is UG or Merge, hence the capacity of recursion that allows to process linguistic information hierarchically. Finding the biological and genetic bases of this trait will allow to explain language evolution.

A confirmation of the application of this approach to language evolution is represented by the fact that the discovery of FOXP2 human variant was welcomed in the 1990s as the "language gene", and still today this erroneous label is simplistically used in both popular and scientific journals (see Box 1 and paragraph 5).

Box 1 – FOXP2
FOXP2 is a protein belonging to a family of transcription factors (Forkhead bOX or FOX) regulating the expression of suites of genes during embryogenesis and development and in adulthood in different tissues (see Ramus and Fisher, 2009). In the 1990s an interesting case-study was reported: members of the KE family (15 individuals across 3 generations) were shown to display a severe speech and language disorder, in particular Developmental Verbal Dyspraxia (DVD) (impaired tongue, lips and jaw movements, impairment in ordering sounds in correct sequences and in pronouncing words correctly), inherited as a Mendelian trait with an autosomal dominant mode of transmission. Analyses of the FOXP2 genes revealed heterozygous single-base change in all 15 affected members, which was not found in any unaffected members and controls. Moreover, FOXP2 has been found to regulate the expression of CNTNAP2 gene (located on chromosome 7q35) in neurons; allelic variants of this target were shown to be associated to Specific Language Impairment (SLI). More insights on the role of FOXP2 came from comparative studies. Mice carrying the same mutation as that found in KE family members display abnormal synaptic plasticity were FOXP2 is expressed and significant motor-skill deficits in species-typical behaviours and they do not emit innate calls in isolation from their mothers (Groszer et al., 2008). Convincing evidence of a role for FOXP2 in vocalization skills of nonlinguistic species comes from studies of vocal learning in songbirds, in particular zebra finches where expression of FOXP2

in Area X correlates to vocal plasticity (White *et al.,* 2006) and to inaccurate and incomplete copying of the tutor's song, which was suggested to show parallels to DVD in humans (Haesler et al., 2007).

Analyses of the evolution of FOXP2 in primates indicated that two amino-acid substitutions occurred on the human lineage after splitting from the chimpanzee, and found evidence of recent Darwinian selection (Enard et al., 2002). However, the same FOXP2 variant was found in Neanderthal genetic analyses (Krause et al., 2007), suggesting a more ancient origin (300-400 kya).

Overall, these comparative data suggest that FOXP2 plays a role related to motor sequencing and vocal learning. However, FOXP2 cannot be regarded as "the language gene" as it is just one of the multiple bricks that build up the language mosaic.

3. External Language, social selection and functional hypotheses

In the following years several hypotheses on language evolution were proposed (for a review see Szamado and Szathmary, 2006), shifting the focus of attention from I-L to E-L; in a nutshell, researchers started considering language in a primarily social dimension, hence object of social selection. These kind of hypotheses, contrarily to the non-functionalist or structuralist Chomskian explanation, represent examples of functional hypotheses for the origin and evolution of language.

For example, primatologist Robin Dunbar, who found statistical correlation between brain size and dimension of the social group in primate evolution (see Dunbar and Shultz, 2007), proposed the "grooming hypothesis" for the evolution of language (Dunbar, 1996). Primates maintain social bonds by manual grooming, however this is a costly activity as it occupies both hands and precludes other activities such as foraging or feeding. According to this hypothesis, as group size increased, vocal grooming substituted manual grooming, giving the advantage to groom more than one individual at once and giving the opportunity to perform other tasks simultaneously. First vocalizations were not meaningful, much like contact calls in geladas and other primates. It was only with *Homo sapiens* that meaning entered the evolutionary scene, with symbolic language considered as the last step allowing reference to abstract concepts.

By stressing continuity with primate communication systems, Dunbar is not able to provide a specific explanation for the alleged species-specific features of human language such as the hierarchical structure of phonology and syntax (also called duality of patterning, that is phonemes merging into words and words merging into sentences; see Fitch, 2010).

However, the largest difference with Chomskian UG hypothesis is that the attention is here switched to other components of the language faculty, such as meaning and symbols, and not only syntax.

Many hypotheses of this kind (functional hypotheses relying on social selection, hence giving evolutionary relevance to E-L) were proposed across these years (Dessalles, 1998; Donald, 1991; Deacon, 1997; see Szamado and Szathmary, 2006 for a review) and some criteria have been elaborated to evaluate the strength of such hypotheses.

For example, a good evolutionary hypothesis should solve the problem of honesty, that is, explaining why there should be a shared interest among individuals to communicate, hence to cooperate sharing useful or adaptive information, avoiding at the same time cheaters to take advantage. A large amount of literature has been produced around the honesty problem and it is not the aim of this work to review it all here.

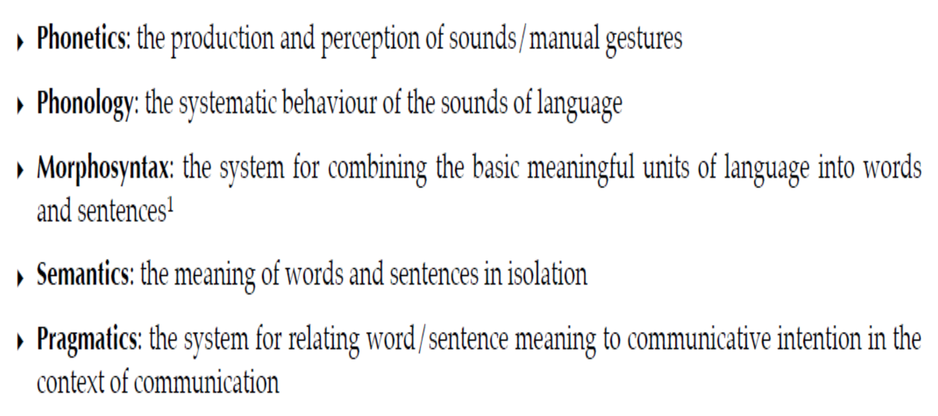
Although language evolution is tackled from its external component in the works reviewed in Szamado and Szathmary (2006), these hypotheses still share a common explanatory structure characterized by an atomistic approach, that is isolating a single component, and a monofunctional explanation, that is attributing to this component a precise function (gossip, grooming, hunting, mating, etc., see Szamado and Szathmary, 2006) that is considered responsible for the whole evolution of language.

However, the critique that can be moved to this type of explanations is that these hypothetical scenarios are not proper evolutionary explanations, as functional explanations alone are not sufficient to characterize a full evolutionary explanation. In fact, following Tinbergen 4 Qs (Tinbergen, 1963), the functional explanation is just one of the aspects that should be inquired in order to obtain a proper comprehension of the evolutionary origin of a trait. Reducing an evolutionary explanation to its functional aspects is a simplified representation of the evolutionary process and represents what Stephen J. Gould labeled *just so stories*. The hypothetical functional scenario must be met with the historical side of the evolutionary explanation; in this sense, integrating what we know from the archeological and fossil record (in the case of human evolution and the origin of language), as well as with the alleged structures and the mechanisms involved, is a crucial aspect that has often been overlooked in many proposed hypotheses for the evolution of language.

4. A tentative definition for the language faculty: FLB – FLN

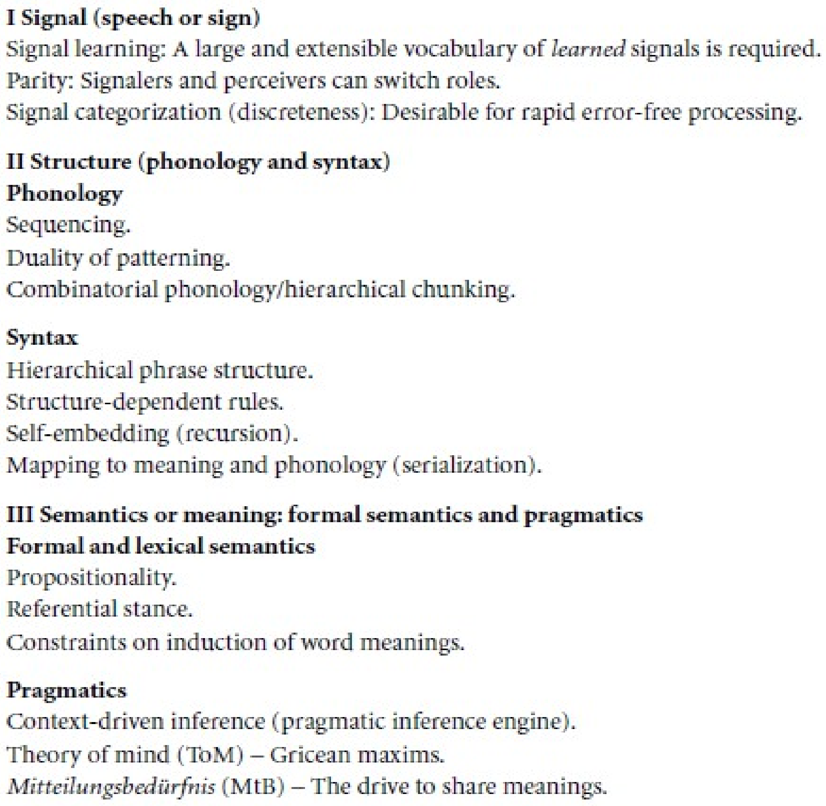
All these studies in language evolution produced the positive effect of widening the components of the language faculty that should be considered in the evolutionary analysis beyond the only recursive property of syntax that, as an effect of the influent chomskian legacy, in the previous years was equated to the language faculty itself. As a matter of fact, some scholars stick with this ultra-narrow definition of language still today (Bolhuis *et al.*, 2014, 2015; Berwick and Chomsky, 2016).
Language is an extremely complex trait whose evolutionary building up involved genetic, morphological, neural, cognitive, behavioral and cultural change. The definition of the object of inquiry and the research method employed for its investigation are elements that go side by side. Finding a definition able to keep together all these aspects is at the same time a very hard and a crucial task. The goodness of a definition can be evaluated on the fecundity of the associated research program it is able to generate.
Hauser, Chomsky and Fitch (2002) tried to put order to the various components of the language faculty, proposing a categorization based both on linguistic and biological criteria (see also Fitch, 2010). According to their proposal, the language faculty can be subdivided into:

1) its sensory-motor component (signal: speech or sign)
2) its conceptual-intentional component (semantics and pragmatics)
3) its abstract computational component (syntax and its recursive property)



- **Phonetics**: the production and perception of sounds / manual gestures
- **Phonology**: the systematic behaviour of the sounds of language
- **Morphosyntax**: the system for combining the basic meaningful units of language into words and sentences[1]
- **Semantics**: the meaning of words and sentences in isolation
- **Pragmatics**: the system for relating word / sentence meaning to communicative intention in the context of communication

Figure 1
From Kirby (2007). A schematic view of the role played by the main components of the language faculty allowing language to generate unbounded yet faithful transmission of information (discrete infinity).



I Signal (speech or sign)
Signal learning: A large and extensible vocabulary of *learned* signals is required.
Parity: Signalers and perceivers can switch roles.
Signal categorization (discreteness): Desirable for rapid error-free processing.

II Structure (phonology and syntax)
Phonology
Sequencing.
Duality of patterning.
Combinatorial phonology/hierarchical chunking.

Syntax
Hierarchical phrase structure.
Structure-dependent rules.
Self-embedding (recursion).
Mapping to meaning and phonology (serialization).

III Semantics or meaning: formal semantics and pragmatics
Formal and lexical semantics
Propositionality.
Referential stance.
Constraints on induction of word meanings.

Pragmatics
Context-driven inference (pragmatic inference engine).
Theory of mind (ToM) – Gricean maxims.
Mitteilungsbedürfnis (MtB) – The drive to share meanings.

Figure 2.
From Fitch (2010). The Three "Ss" of the faculty of language: Signal, Structure and Semantics. Each of this component can be further subdivided into multiple separate but interacting mechanisms; for an example see the role of gaze processing in Theory of Mind (Fitch et al. 2010)

Signal, Semantics and Syntax are labeled the three "Ss" of the faculty of language (see fig. 1 for a schematic description of the main components; see fig. 2, from Fitch, 2010). These components, however, are further categorized according to the comparative method into two groups. The sensory-motor and the conceptual intentional component belong to the *Faculty of Language in a Broad sense* (FLB). This set contains all those elements of the language faculty that are involved in language, but that are not exclusively present in humans. An example is represented by the relatively wide distribution in the tree of life of vocal learning, the capacity to imitate, elaborate and reproduce acoustic sounds learned from conspecifics: beyond humans (the only primates possessing it), songbirds, parrots, hummingbirds, cetaceans, pinnipeds, bats, elephants and possibly goats possess it (Petkov and Jarvis, 2012). The recursive property of syntax instead is proposed to belong to the *Faculty of Language in a Narrow sense* (FLN), that is intended as a subset of FLB containing the component(s) that makes language a human species-specific characteristic, not shared with other animals. Elements should be assigned to each set with no a priori assumptions, but only after empirical evaluation. This definition in fact allows to exploit the explanatory power of the comparative method as the distinguishing criterion and research roadmap (see for example Fitch *et al.*, 2010).

However, the authors explicitly proposed recursion, hence the capacity for discrete infinity, to be the alleged uniquely human characteristic that distinguishes language from any other forms of animal communication, exposing their proposal to falsifiability. They also advanced an exaptationist hypothesis for the evolution of recursion: they don't consider it as a specific adaptation for linguistic tasks, as they conceive it as a characteristic with tenuous connections with communicative efficiency, in line with the traditional Chomskian view. Instead they suggest that these computational properties evolved for reasons other than communication (even if without clearly specifying them) and that they were exapted only in a second stage for linguistic tasks.

The distinction between FLB and FLN allows to see the language faculty not as a single trait (such as when language is equated to UG) but rather as a mosaic of traits, with several subcomponents (multicomponent approach, see Fitch, 2012) that can be ordered by applying a comparative criterion. A certain subcomponent can be found in different species, belonging to different vertebrate taxa; a case by case evaluation will tell us whether it results from convergent evolution or homology, whether it evolved as a specific adaptation or rather it derives from extant structures exploited for novel functions (exaptation). This in principle should help understanding how language, intended as a complex cognitive trait, came together as we know it today.

If we take into account the three main domains of the language faculty (speech, semantics and syntax, following Fitch, 2010 categorization), we can provide for each one of them some examples of the productivity of a multicomponent and comparative approach:

1) Speech: it has been shown that the descent of the larynx may not necessarily be a specific adaptation for speech as many animals among mammals possess this analogous trait (Lieberman, 1984; Fitch and Reby, 2001; Weissenburger *et al.*, 2002). This comparative analysis provides data that can help understanding the evolutionary path followed by human larynx, which possibly descended for reasons other than speech and only later was exploited for speech-related functions. Vocal learning also proves to be a rather convergent trait among some distantly related vertebrate taxa (Nottebohm, 1976; Janik and Slater, 1997; Petkov and Jarvis, 2012). Shedding light on the selective pressures which favored this trait may help understanding why humans are the only bearers among primates. However, it must be said that it is more and more acknowledged that a all-or-nothing approach to the presence of a trait in a certain species is leaving room in the latter studies to a bottom-up approach (see de Waal and Ferrari, 2010) according to which it is possible that a certain trait, such as vocal learning or theory of mind, can be present in different degrees in different species.

2) Semantics: an example of the productivity of a comparative and multicomponent approach is

represented by the possibility of constructing *cognitive phylogenies*: a preliminary cognitive phylogeny of vertebrate gaze sensitivity and processing has been proposed for some subcomponents (gaze detection and gaze following) of a key component (theory of mind – TOM) of the semantic and pragmatic domain of the language faculty (Fitch *et al.* 2010). Understanding how such components are distributed among taxa and how they are intertwined into one single species helps figuring out which evolutionary steps have been made to reach a certain cognitive capacity (attention and basic forms of TOM, in this case), shedding more light on how the language faculty is complexly arranged.

3) Syntax: much has been debated on whether the recursive properties of syntax (hence *Merge*) are unique to humans or shared with other species. Although it has been argued that the European starling is able to handle recursion (Gentner *et al.*, 2006), other scientists suggested such a claim is premature (Beckers *et al.*, 2012). Once again the solution to this puzzle lays in relying on the comparative analysis, suspending any *a priori* stance, producing testable hypotheses and letting the empirical results speak (see fig. 3).

Extensive application of the comparative method and accurate analysis of the components of the language faculty showed that the three main components of the language faculty (speech, semantics and syntax) are themselves made up of subcomponents. Results of comparative work in social cognition for example revealed that species distantly related to humans (like crows) show cognitive abilities that are lacking in primates (Fitch *et al.*, 2010). This kind of work has the merit to show the inadequacy of a *scala naturae* view of evolution according to which cognitive abilities increase in the approximation to humans. A modern Darwinian viewpoint instead assesses that each species cognitive abilities evolve to fit the demands of its ecological niche.

5. Problems with FLB – FLN

FLB – FLN distinction had the merit to put the language faculty in the tree of life, treating language not as a monolith, but rather as a mosaic of traits, each of which might in principle have had different evolutionary paths, might have being present in different degrees in different species (bottom-up approach, see de Waal and Ferrari, 2010), might have emerged different times in phylogeny (convergent evolution), or might have being present in the common ancestor of a group of species (homology). The explanatory potential of the comparative and evolutionary analysis is displayed here.

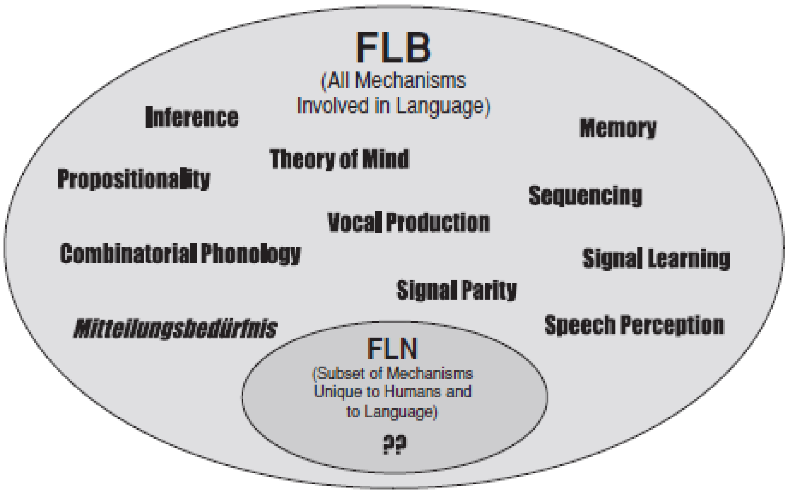


Figure 3.
From Fitch (2010).
The faculty of language in broad and narrow senses: two ways in which the term "language" can be used. FLB (faculty of language in the broad sense) is the all-inclusive sense, incorporating any mechanism that is involved in language processing. FLN (faculty of language in the narrow sense) is the exclusive sense: by definition it includes only that subset of mechanisms that are both specific to humans, and specific to language within human cognition. Only a small subset of language-related mechanisms are expected to be in the latter category.

However, a problem with FLB definition is represented by the fact that this group contains all those components of the language faculty that are not exclusively present in humans, so either they are inherited from ancestors or they are present in other animals. However the definition of FLB remains unclear on which of the two alternatives is correct.

Moreover, the recursive property of syntax for example were thought to be a uniquely human characteristic, but different studies today found that different species of birds can master recursive properties in signal processing (Gentner *et al.*, 2006; Suzuki *et al.*, 2016; Spierings and ten Cate 2016). If these studies are correct, recursion, believed to be the element filling the FLN set, should be moved to FLB set, leaving FLN an empty set and challenging the usefulness of the dinstinction between FLB and FLN.

However, given the actual uniqueness of human language as a communication system in the animal reign, it is legitimate to expect some forms of specificity. A solution to overcome this difficulty was presented by Okanoya (2007), arguing that FLN should be intended not as a single trait unique to humans, but rather as a unique-to-humans combination of not unique traits.

Moreover, it must be said that the original multicomponent approach was affected by a top-down inclination. Intending syntax as an all-or-nothing characteristic, as Chomskian UG implies, leads necessary to treat it as a monolithic trait, long considered to be the species-specific characteristic that conferred full-developed language to humans.

> “Over the last few decades, comparative cognitive research has focused on the pinnacles of mental evolution, asking all-or-nothing questions such as which animals (if any) possess a theory of mind, culture, linguistic abilities, future planning, and so on. Research programs adopting this top-down perspective have often pitted one taxon against another, resulting in sharp dividing lines. Insight into the underlying mechanisms has lagged behind (…). A dramatic change in focus now seems to be under way, however, with increased appreciation that the basic building blocks of cognition might be shared across a wide range of species. We argue that this bottom-up perspective, which focuses on the constituent capacities underlying larger cognitive phenomena, is more in line with both neuroscience and evolutionary biology.” (de Waal and Ferrari, 2010, p. 201)

This bottom-up approach is apparent in studies on vocal learning. The field has long been neatly divided into vocal learners and non-vocal learners. However, recent studies showed much more variability in vocal learning across species (Petkov and Jarvis, 2012; Arriaga *et al.*, 2012), suggesting that it cannot be intended as an all or nothing trait. Rather, both birds and mammals show some minimum level of vocal learning capacities (such as mice, see Arriaga *et al.,* 2012), but only a few groups evolved independently full-developed capacities in response to specific regimes of selective pressures (Jarvis, 2006). For example, predation rates are an important factor: humans, dolphins and killer whales stand on the top of their food chain and predation-related pressures are relaxed; hummingbirds evolved good escape behaviors allowing them to lower pradation rates (Jarvis, 2006); in a domesticated condition, hence in a condition with low predation-related selective pressures, male individuals of Bengalese Finches developed more complex songs and female preference reinforced this tendency (Okanoya, 2012). We will discuss the plausibiity of the Self-domestication hypothesis applied to human evolution in the first chapter of this work (Suman and Pievani, 2015). Nowicki and Searcy (2014) also showed that vocal learning maintenance is favored within a population when the trait is already present in the population in a certain degree. We will discuss in chapter three (Suman, submitted) and in the conclusions of some aspects of a frequency dependent model of selection.

The same top-down approach was once applied to other cognitive traits such as Theory of Mind, the capacity to understand other individuals belief and intentions. Premack and Woodroof (1978) in their influential paper asked whether chimpanzees had a theory of mind, answering in the negative.

Researchers in the following years outlined that this cognitive trait cannot be intended and inquired as an all-or-nothing trait, but it is given in different degrees: for example, Call and Tomasello (2008) conclude that chimpanzees understand others in terms of perception-goal psychology, while humans in terms of a belief-desire psychology.

As a consequence of these considerations, speech, semantics, syntax, intended as monolithic subcomponents (as it is in the FLB – FLN distinction) of the language faculty might represent a rather simplistic account.

Nonetheless, this distinction was adopted to formulate hypotheses on possible protolanguages that our non-human primate ancestors might have possessed (see Fitch, 2010). There are three main hypotheses on possible protolanguages:

1) *lexical*: described as individual words unconnected by syntactic rules (Bickerton, 1990);
2) *gestural*: intended as a manual/visual modality of communication that preceded the auditory/vocal modality (Rizzolatti and Arbib, 1998; Corballis 1999);
3) *musical*: conceived as a communication system in which phonology and syntax were present but propositional meaning of sounds was lacking (Darwin 1871, Fitch 2006).

Each of them hypothesizes a different evolutionary sequence of the three main components of the language faculty, and consequently different type of communication systems:

1) *lexical*: speech, semantics, syntax;
2) *gestural*: semantics, syntax, speech;
3) *musical*: speech, syntax, semantics.

Despite resulting intuitive, this categorization might result rather simplistic and still limited by a top-down approach. Moreover, the original categorization (Hauser, Chomsky, Fitch, 2002) doesn't include pragmatics (somehow reduced to semantics) while the latter is included in Fitch, 2010 (see figure), after recent studies that put it in light as a key component of the evolution of language (see Scott Phillips, 2015).

The original definition of FLB (Hauser *et* al., 2002) also didn't include general systems not specifically evolved for language such as memory, while the latter is included in Fitch, 2010 (see fig. 3). This might seem as a sign of weakness of the definition as it becomes too inclusive and rather unspecific.

Another critical point of FLB – FLN distinction, highlighted in Boeckx (2014), is how to categorize novelties. FOXP2 for example belongs to a highly conserved family of transcription factors, but it has been subject of two significant mutations in the human lineage and in humans it is involved in specific linguistic functions, as documented by the Devolopmental Verbal Dyspraxia in the KE family showedin *Box 1*. In which set should FOXP2 be assigned? If its specific involvement in language tasks in humans is considered, FLN would be the answer (Boeckx, 2014), but according to Fitch *et al.* (2005) the highly conserved nature of this transcription factor prevails on its functional specificity, assigning it to FLB. If we stick with Okanoya's proposal of considering FLN as a combination of traits, still FOXP2 could be arbitrarily assigned to one set or the other, without a clearcut criterion.

Given this difficulties, given the elusiveness of FLN, being said that only a wide application of the comparative method could assess the composition of the language faculty ("quantitative" approach), the FLB – FLN distinction seems to remark a qualitative distinction between what is shared (synapomorphies) and what is derived (apomorhpies) which is unnecessary: in evolution there is nothing special in being special, given that this is just what descent with modification is all about. Finding species specific traits does not make their possessors qualitatively different from their ancestors and their relatives.

Moreover, Hauser *et al.*, 2002 FLB – FLN distinction conceived the idea that cognitive evolution occurs via accumulation of novel components (FLN) on a set of pre-existing ones (FLB), that is adding novel characters on top of others. This probably obscures the idea that new cognitive traits could emerge even without the appearance of *de novo* or unique adaptations, but only via a reorganization of the already existing cognitive traits. Stephen J. Gould already suggested that the brain has undergone massive exaptive processes (Gould, 1991). *Neural reuse* is the mechanism through which a same neural area could be recruited in different circuits performing different tasks; this exaptive principle might have played a significant role both in development and in evolution (Anderson, 2010). Okanoya's proposal of considering FLN as a combination of traits is in principle an attempt to preserve FLB – FLN distinction against a "cumulative" view of cognitive evolution and in favor of an exaptationist view based on a re-organization of existing features.

6. Cultural evolution and the innate-acquired problem

Despite displaying the explanatory power of the comparative method, FLB – FLN distinction carries around some problems connected to a conception of language influenced by Chomskian legacy. An *ultra-narrow* definition of the language faculty, stressing language uniqueness and arguing against the usefulness of the comparative analysis, is still defended today (Berwick *et al.*, 2013; Bolhuis *et al.*, 2014, 2015; Berwick and Chomsky, 2016). So the debate is far from its resolutive endpoint.

Supporters of a strong biological determination of language tend to state that the alleged universal features of world languages (such as "word order", that is the sequence of Subject, Object and Verb in a grammar) are engrained in a biologically inherited language acquisition device that constraints language acquisition within certain innate parameters.

Recent studies in the field of historical linguistics (a comparative and historical approach to world languages adopting phylogenetic methods of analysis) seriously challenge the idea that all world languages share universal features such as word order (Dunn *et al.*, 2011). Some studies show that cultural evolution is the primary factor that determines linguistic structure, in respect to word order, showing that different language families (Indo-European, Austronesian, Bantu and Uto-Aztecan) display different word order organization (Dunn *et al.*, 2011).

Other studies (reviewed in Evans and Levinson, 2009) show that this variability is not limited to word order, but rather is extended to almost every other level of description, such as sounds, meaning, lexicon and even syntactic organization, which shows compelling variability. The concept of UG is hence considered hindering the appreciation of such fundamental structural differences among languages (Evans and Levinson, 2009).

Such an intuition was already present in Deacon (1997):

"Grammatical universals exist, but I want to suggest that their existence does not imply that they are prefigured in the brain like frozen evolutionary accidents. In fact, I suspect that universal rules or implicit axioms of grammar aren't really stored or located anywhere, and in an important sense, they are not *determined* at all. Instead, I want to suggest the radical possibility that they have emerged spontaneously and independently in each evolving language, in response to universal biases in the selection processes affecting language transmission." (Deacon 1997:115-116)

A series of studies performed by evolutionary linguists from the University of Edinburgh in the last 20 years seems to rise serious challenges to the *nativist* account of language, according to which the syntactic features of languages can be traced in the recursive properties of a language acquisition device, biologically determined and inherited. Simon Kirby and colleagues proposed a radically different explanation for compositional syntax as the outcome of dynamics of learning and information transmission among individuals (Kirby 1998). The Iterated-Learning-Model (ILM) is the approach developed by Kirby and colleagues.

Iterated learning is a process in which an individual acquires a behavior by observing a similar behavior in another individual who acquired it in the same way. Models of this process show that, over repeated episodes of transmission, behaviors transmitted by iterated learning tend to become easier to learn and increasingly structured (Kirby *et al.*, 2008).

ILMs consist mostly in computer simulations of transmission dynamics among agents provided with some specified but rather general learning bias (for example defined as Bayesian inference in Kirby *et al.*, 2007). The linguistic behavior a learner is exposed to as an input is itself the output of learning by other individuals. Similarly, the language spoken within a population at a generation is the learning input for the subsequent generation. Language is hence intended as a population-level phenomenon whose characteristics are shaped along the cultural transmission processes (see fig. 4).

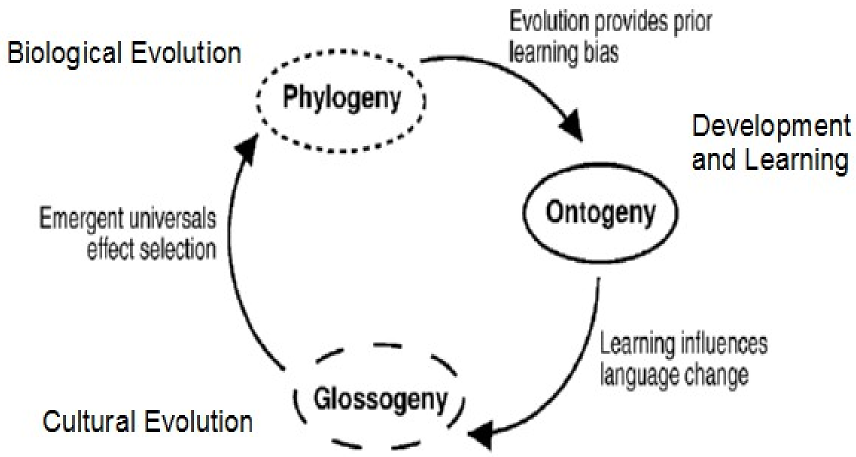


Figure 4.
From Kirby (2002).
Cultural evolution is intended as the process that produces change in languages in time, but more generally that transmits behaviors through social learning across generations. This time-scale of change is often labeled the glossogenetic *level (Fitch, 2008) and it interacts with the learning mechanisms at the* ontogenetic *level and with biological evolutionary processes occurring on a* phylogenetic *timescale: language emerges as the complex intersection of these processes occurring at different timescales.*

ILM experiments assume Chomskian distinction between I-L (patterns of neural connectivity constituting the biological substratum for abstract grammars) and E-L (the actual sets of utterances through which languages take form) as the fundamental model through which languages exist and persist (Kirby and Hurford, 2002). However, differently from Chomskian cognitivist internalist approach all focused on I-L as the fundamental device building and constraining languages and their structure, leaving E-L as a secondary aspect not relevant to understand language structure, evolutionary linguists show how cultural transmission dynamics of E-L can shape language structure, stating in particular that "cultural evolution leads inevitably to recursively compositional (i. e. syntactic) languages" (Kirby and Hurford, 2002).

Compositionality or *compositional syntax* is the property of human language whereby semantic units (like words) are combined into larger compounds (phrases and sentences) whose composite meanings are functions of, but not wholly determined by, the independent units (Bowling and Fitch, 2015). "Languages with compositional syntax assign signals to meanings in a predictable and systematic manner; in other words, they use the same encoding strategy for every meaning. An evolutionarily early form of protolanguage that has been hypothesized (Wray, 1998) has no such systematic syntax, but instead treats every meaning holistically. In such a protolanguage, the signal for every meaning must be learned individually, and no generalizations are possible" (Kirby *et al.*, 2007). This property is commonly thought to be the hallmark of human language with no animal communication systems showing it (although see Gentner *et al.*, 2006; Suzuki *et al.*, 2016). UG has long been retained the explanation for this property of language, but Kirby and colleagues' work claims that compositionality (along with *sistematicity* and *learnability*) might arise from cultural transmission dynamics without assuming specific cognitive learning biases in the individuals and without the action of natural selection, intended as selective pressures acting on genes controlling for a specific trait (Kirby, 1998).

In order to persist from one generation to the next, a language must be mapped from I-L to E-L through use, within an individual, and from E-L to I-L through learning (transmission) among individuals. In order to "reproduce" from one individual to the other, languages should be learnable, that is their structure should fit individuals' brains and cognitive biases. The spontaneous emergence and persistence of certain linguistic forms is intended as "cultural selection for learnability" according to these cultural transmission dynamics from individual to individual and across generations (Brighton *et al.*, 2006).

The idea of languages' *learnability* at the basis of language reproduction and diffusion was one of the fundamental intuitions that inform Terrence Deacon's 1997 work *The Symbolic Species: the co-evolution of langauge and the brain*.

"The most basic principle guiding [language] design is not communicative utility, but reproduction – theirs and ours. (…) Languages are social and cultural entities that evolved to the forces of selection imposed by human users. The structure of a language is under intense selection because in its reproduction from generation to generation, it must pass through a narrow bottleneck: children's minds" (Deacon, 1997, p. 110)

Languages can be metaphorically intended as entities that adapt to survive by fitting to learners' mind, that means adapting to be learnable (Brighton *et al.*, 2006). Kirby and colleagues' experiments on ILM show that this language adaptation to learnability can occur without any change in individuals' prior learning biases or any biological change (Kirby *et al.*, 2007; Kirby *et al.*, 2008; Kirby, 2014).

"In particular, the experiments of Kirby (2002b) and Batali (2002) demonstrate that a collection of learners (…) will, from an initially holistic communication system, spontaneously arrive at compositional and recursive communication systems. Because language is ostensibly infinite, and cultural transmission can only result in the production of a finite series of utterances, only generalisable forms will survive. These experiments suggest that certain hallmarks of language are culturally adaptive: pressures arising from transmission from one agent to another cause these hallmarks to emerge and persist. For example, adaptive properties such as compositionality and recursion, which we can consider absolute language universals, are defining characteristics of stable systems" (Brighton *et al.*, 2006, p. 10).

The majority of the studies performed by the Scottish evolutionary linguists are computer simulations of learning dynamics (reviewed in Steels, 2006). The same type of model however was transferred in the lab with human learners, in a diffusion-chain experiment (Kirby *et al.*, 2008). Participants are exposed to artificial language learning and the learning input of each participant is the output produced by the previous participant according to what he/she learned. In order to make the language more learnable, compositional structure emerges spontaneously as the unintentional product of transmission, as participants (unaware of the problem) were trying to reproduce as best as they could the artificial language they were exposed to. The authors conclude that "just as biological evolution can deliver the appearance of design without the existence of a designer, so too can cultural evolution" (Kirby *et al.*, 2008).
Although it is recognized that genes may code for learning biases, in Kirby's models selection is acting on what they define as the extended phenotype of language, that is those properties that emerge at the population level as a result of cultural transmission.

"This approach does not deny the possibility that much of our linguistic ability is genetically coded and may be explained in terms of natural selection, but it does highlight the fact that biological evolution is by no means the only powerful adaptive system at work in the origins of human language" (Kirby, 1998, p. 1)

In Chomskian view, language is seen as an individual trait (I-L), a cognitive device mapping signals into a representation system assigning meaning to them according to a set of syntactical rules biologically engrained. The role of the linguistic population is not considered as a relevant factor in determining language structure: language universals are to be explained with the innate cognitive biases shared by all the world speakers.

Although putting a final word on the fruitfulness of UG as the fundamental engine for language acquisition is not the aim of this work, as this debate belongs to the linguistic framework, it is interesting to note how Kirby's studies stress the importance of cultural evolution as a factor shaping language. ILM studies challenge the existence of strongly constraining biological predispositions for language and the adaptationist view according to which language structure was shaped by natural selection (Pinker and Bloom, 1990) acting on the alleged biological constraints, whose very existence is questioned by the ILM simulations and experiments.

Some clarifications however are needed. The object of inquiry of ILMs is language structure, that is language current features and universals. This is something different from the language faculty, as intended by Hauser *et al.* (2002). ILM propose the alternative explanation that language current features, such as the much debated and fundamental trait of compositional syntax, are not determined by innate learning constraints, biologically evolved, but rather they are the outcome of language use, cultural transmission dynamics that shape language in order to make it more learnable: language structure is a function of its learnability, the characteristic that allows language to "reproduce" and "survive" (be transmitted from individual to individual and across generations).

Cultural evolution, an evolutionary process acting on a different timescale, other than biological evolution and classical natural selection, is retained responsible for the emergence of a property (compositional syntax) that Chomsky explained with UG (without providing a satisfactory evolutionary explanation) and Pinker and Bloom explained with natural selection (a functional explanation).

Evolutionary linguistics studies seem to lead to the consequence that two independent evolutionary processes are responsible for a trait whose complexity is growing even bigger: not only language should be intended as a mosaic of traits, each of which might have had an independent evolutionary history (*multicomponent approach*), but also different evolutionary processes acting on different timescales are responsible of language evolution; this means that, in order to explain the evolutionary emergence of this trait, we have to consider evolutionary processes that differ fundamentally in nature (*explanatory pluralism*) (see Box 2).

Box 2 – biological and cultural evolution: differences and analogies

Biological and cultural evolutionary processes share analogies and differences. Both processes can be described as sharing a common bones that is typical of all Darwinian processes: 1) variation 2) inheritance 3) differential survival. However, some fundamental differences exist as well: if variation is usually believed to be random in biological evolution (new mutations emerge randomly in the population), in cultural evolution variation can be biased and even intentionally directed towards specific novelties. Some fundamental differences are present also in the system of inheritance; while in biological evolution inheritance is *vertical* (from one generation to another), in cultural evolution there are multiple modalities through which cultural information can be transmitted: vertical (from parents to offspring), horizontal (between two individuals of the same generation), oblique (from one individual of one generation to a non-related individual of another generation) (see Cavalli Sforza and Feldman, 1981). Moreover, while selection is one of the most important processes through which a trait persists in biological evolution, some researchers believe that selection is not as fundamental in cultural evolution as it is in the biological domain; in fact, they maintain that the persistence of a cultural trait follows a modality that they call it the *cutural attraction* model and selection is considered a subset of the possible forms that attraction can take (Cladiere et al. 2014). Moreover, biological evolution and cultural evolution fundamentally occur on different timescales, the latter being much faster than the former. The debate on how to frame cultural evolution and understanding to which extent it shares fundamental features with biological evolution is open and alive today. For an introduction to this topics see Mesoudi (2011).

Uncovering the genetic underpinnings of language remains a crucial effort and the biolinguistic program (Boeckx *et al.*, 2012) is trying to do exactly so, stressing the importance of identifying the genetic and epigenetic network at the bases of language, focusing in particular on the concept of language-ready brain, which is thought to be shaped by biological evolution during human evolution (Arbib, 2012; Boeckx and Benitez Burraco, 2014). However, we would like to stress that understanding the relationships between biological evolution and cultural evolution is crucial for understanding the dynamics at the bases of language evolution and origins. We argue that such integration is much needed.

We will consider now some studies that address the interaction between biology and culture in language evolution bringing arguments in favor of a separation and a sort of incompatibility between biological and cultural evolutionary processes.

7. Biology and culture: different evolutionary rates

A strong argument against an adaptationist account of language evolution, say à la Pinker and Bloom, comes from the "moving target" argument held by Christiansen and Chater (2008).

Language change rate occurs on a timescale that is considered incompatible with the timescale on which natural selection operates, hence the claim that a universal feature of language would be coded in genes, fixed by natural selection, is unsustainable: natural selection cannot simply lead to genetic fixation a trait that is changing too fast. Hence it results highly improbable that a domain-specific mechanism could have evolved as an adaptation via the slow and gradual action of natural selection (Christiansen and Chater, 2010). These authors also dismiss as highly implausible the non-functional account of language (Bickerton, 1995; Gould, 1993; Lightfoot, 2000) intended as a by-product of some structural effect such as increase in brain size (Christiansen and Chater, 2008).

However, it has to be noticed that the critique to the adaptationist view of UG itself adopts a naïve evolutionism when it assumes a one-to-one correspondence between genetic change and linguistic features. Moreover this critique seems to conflate the nature of UG, treating it as a feature common to all languages (E-L) and not as a cognitive computational device that allows to acquire language (I-L).

Christiansen and Chater conclude that UG represents a domain-specific system for language for which no viable evolutionary account is available. Instead of viewing the brain as having a genetically evolved system for language, they propose that the key to language evolution is the evolutionary process over language itself. Language features that are easy to learn and process or communicatively effective will be retained; language is the way it is not because of a domain-specific language acquisition device, but rather because of domain-general cognitive biases already present in the brain and not specifically dedicated to language, from which the motto: "language as shaped by the brain" or language adapted to the brain (Christiansen and Chater, 2008).

The nature of these constraints is divided into four groups: perceptuo-motor factors, cognitive limitations to learning and processing, constraints from thought, pragmatic constraints (see Christiansen and Chater, 2010 for details, where the implications for language acquisition are also discussed).

The incompatibility between biological and cultural evolution is made explicit in this passage:

“Cultural evolution will work against biological (co)evolution in the case of malleable aspects of culture— rapid cultural change leads to a fast-changing cultural environment, which serves as a ‘‘moving target’’ to which biological adaptation cannot occur” (Christiansen and Chater, 2010, p. 12).

Based on computer simulation (Chater et al., 2009), they argue that “genes encoding aspects of culture that were initially freely varying, and *not held constant by functional pressure*, could not have arisen through biological evolution” (Christiansen and Chater, 2010, p. 12, my italic)
As biological and cultural rates of evolution are considered incompatible, Christiansen and Chater (2010) consider the two processes as independent; nonetheless, they acknowledge that, to a certain extent, the two processes can interact, displaying the issue in the following way, identifying two clear-cut options:

1) culture comes first and biological adaptation brings about the fit with the cultural structure; they call it *biological evolution*, or biological adaptation to cultural structures.
2) biological structures come first, and cultural adaptation brings about the fit with these biological structures; they call it *cultural evolution*, as culture adapts to pre-existing biological constraints.

According to the “moving target” argument (specifically developed for language, but extensible to cultural behaviors in general) culture does not generate selective pressures consistent enough to allow biological adaptation. Also, point (1) assumes that culture does not arise from biological constraints, that is it is not the product of previous selective events. Moreover, biological adaptation to a cultural environment would produce highly adapted domain-specific mechanisms.
On the other side, point (2) assumes that culture is determined by pre-existing biological and developmental constraints and its evolution adapts to these constraints through processes of cultural variation, transmission and selection. The pre-existing biological machinery is the product of Darwinian selection in relation to old tasks; culture sets new tasks, co-opting already present structures to new functions. In this sense the motto 'language is shaped by the brain' can be generalized in 'culture adapts to biological constraints'.
We believe that this way of framing the problem show limitations, as both these accounts taken separately miss some crucial points.
Point (1) implicitly assumes that in human evolution selective pressures were not held constant, so

that biological adaptation could occur at all. However, we will explore an alternative to this viewpoint: partial genetic assimilation (Dor and Jablonka, 2000).

Point (2) poses a too radical separation between biological and cultural evolution, indirectly suggesting that the former makes its job till a certain point and then the workload is overtaken by cultural evolution. This viewpoint (which we label *separationist* and which is explored and criticized in chapter three, Suman, submitted) is present in literature today, and we believe its core ideas are embodied in the language-ready brain proposals (Arbib, 2012; Pagel, 2012; see also Boeckx and Benitez Burraco, 2014). We believe that this conception represents a rather simplistic account of the interaction between biological and cultural evolution, as it is not in agreement with what we currently know from the paleoanthropological and archeological record, which instead suggests the viability of a co-evolutionary model of genes, biological constraints and culture (Laland *et al.*, 2010).

Summarizing, Christiansen and Chater's point, despite dismissing UG as a domain-specific system at the bases of language acquisition for its evolutionary emergence cannot be demonstrated, argues in favor of innate biological constraints to which language must adapt, intending these constraints to be domain-general.

So despite the argument brought forward against the conception of UG as a domain-specific system, whose evolution remains difficult to prove, seems plausible and convincing, the argument according to which biological and cultural evolution present incompatible rates of change can be challenged by recent researches.

8. The Assimilate-stretch principle

As we just pointed out, Christiansen and Chater's argument suffers a too radical separation between biological and cultural evolutionary processes. We would like to discuss here a conceptual framework in which biological and cultural evolution show a better integration, interacting and influencing each others.

We have reached the point in which the structuralist (Chomskian), the functionalist (reviewed in Szamado and Szathamry, 2006), the domain-specific (Chomsky and Pinker and Bloom) and the domain-general (Christiansen and Chater) accounts show limitations when matched with the evolutionary analysis. We have identified these limitations primarily in the incapability of providing a proper integration between biological and cultural evolution.

Dor and Jablonka (2000) try to re-frame the evolutionary question assuming a different perspective on language compared to Chomskian syntactic-centered account, assigning much more importance to semantics: speakers mentally categorize, or classify, events according to their semantic properties. Natural language, then, is a communication tool which is structurally designed for the communication of a constrained set of meanings, exploiting the vocal-auditory channel (and the visual channel), and as such it has to be evolutionary addressed.

They recognize the functional specificity of language and its universality (all members of our species possess it), but they argue that

“the claim that *specific* grammatical rules and constraints are genetically encoded cannot be reconciled with what we know about *brain structures*: neuroscientists from different disciplines seem to agree that the brain is an organ of extreme *plasticity* and *generality* (cf. Elman et al., 1996; Deacon, 1997), which means that the chances of finding explicit representations of linguistic specificities innately encoded in brain tissue prior to acquisition are very slim” (Dor and Jablonka, 2000, p. 35)

They characterize language as a unique and highly constrained communication system, dedicated to communication of a specifically restricted set of meanings, as the type of meanings that can be expressed are a constrained subset of what can be thought and felt; “in technical terms, semantic categories are a subset of *conceptual categories*” (Dor and Jablonka, 2000, p. 36)

The definition of the object of inquiry defines together the evolutionary questions that must be addressed to understand the so-defined-object.

The evolutionary machinery proposed by Dor and Jablonka consists of a gradual expansion and sophistication of the set of semantic categories, their interactions, and their modes of mapping onto the speech channel.

We believe that Dor and Jablonka reframing of the definition of language allows to display an evolutionary research programme that is able to exploit the explanatory power of the interaction of biological and cultural evolution influencing each other.

The argument exposed by Dor and Jablonka (2000) is labeled the *assimilate stretch principle*, is refined in subsequent works such as Dor and Jablonka (2001; 2004; 2010), Jablonka and Lamb (2005) and Dor and Jablonka (2014), and relies on some key explanatory ingredients such as *plasticity*, *cultural transmission*, *modification of the selective environment* and *genetic assimilation*. We will discuss further these elements in the wider framework of the debate on the evolution of the evolutionary research programme proposed by the supporters of the Extended Evolutionary Synthesis.

Here is an outline of the assimilate stretch principle (see fig. 5; see also Jablonka and Lamb, 2005): in this model a certain behavior is described as a sequence of actions and an animal, like a bird, is capable of learning a sequence of, say, 4 acts culminating in a certain behavior, be it a mating dance or a nest-building behavior. Constraints on the learning capacity are assumed, due for example to memory limitations or other brain features. Constant selective pressures for the efficient performance are also assumed: the faster you learn and the more efficiently you perform, the more advantage you have. Within the population, individuals in which one step of the complex behavior will be genetically encoded will learn faster and will free a slot to further learning, allowing to sophisticate the behavior and new behaviors will spread in the population via social learning, allowing new behaviors to spread and be modified through cultural evolution. If selective pressures remain constant, the genetic mutation will give an advantage to their bearers and will get fixed within the population: this phenomenon is labeled *genetic assimilation* (see Waddington, 1957; see also Dor and Jablonka, 2014). The speed of assimilation is expected to vary in different cases, depending on the intensity of selection, the number of genes involved, and the nature of their interactions.

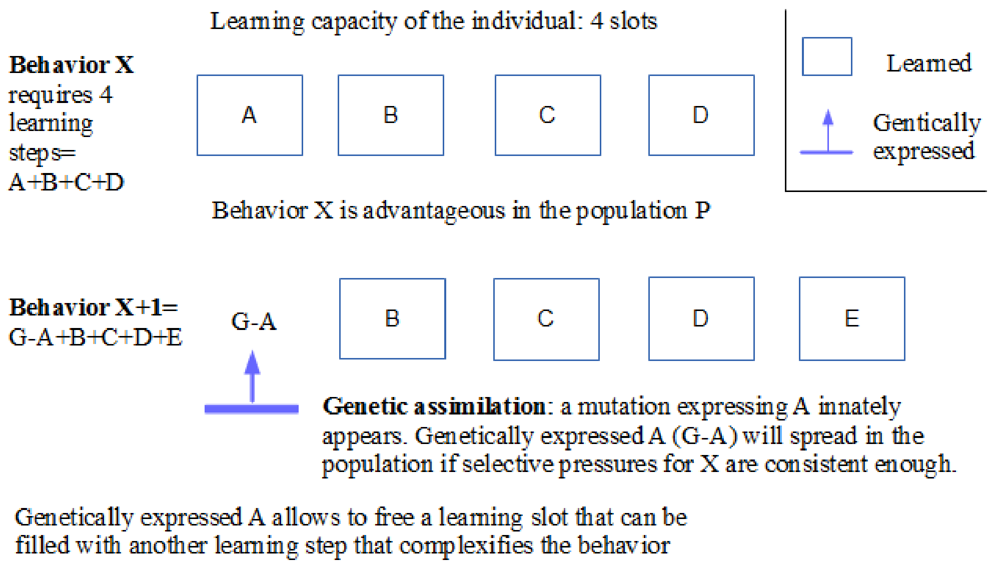


Figure 5. A schematic representation of the Assimilate-stretch principle: a certain behavior (requiring 4 learning steps) is advantageous in the population; a randomly aarisen mutation expressing a step will be selected and will spread in the population if selective pressures remain consistent enough. This allows to free a learning slot and to fill it with a new step: the behavior will grow in complexity.

The process of assimilation of part of the behavioral sequence via genetic evolution and the stretching of the learning sequence may explain the evolution of many behavioral patterns in nature, transforming learned behaviors in more innate, or instinctive, behaviors, such as predator avoidance in birds, poisonous food avoidance in rats or fear of the smell of lions shown by hyena cubs before they have ever encountered a lion (see Avital and Jablonka, 2000). Genetic assimilation is dependent on the consistency of the selective pressures, so it can also occur in only a partial assimilation of the learning sequence. At the same time selection pressure for more efficient learning exposes hidden variation in the ability to learn the specific behaviour, and leads to the selection of better, specialised learners.

This model describes a process that shows the interaction between the biological and the cultural level: the process of genetic assimilation (genetic evolution) and the stretching of the learning sequence and its spread through social learning (cultural evolution).

The type of process described reflects a typical case of Baldwin effect (Baldwin, ; Simpson, 1953). Individuals first adapt to a new environmental challenge with a flexible, plastic accomodation of the phenotype. If selective pressures are constant enough, learning is on average more costly and lenghty then a genetically fixed expression of the same behavior, as the energetic investment will be smaller. If individuals emerge in the population equipped with genetic variations that will lower the learning investment, they will have a selective advantage on those individuals fully relying on learning, as the efficient behavior will be expressed faster and more efficiently. The advantageous genetic variant will spread and fix in the population through standard Darwinian selection.

Applied to the evolution of language, this model assumes a system of a very limited set of meanings mapped onto a set of phonetic markers, similar to an early protolanguage or an animal communication system based on referential calls, such as alarm calls or emotional-social vocalizations, as it is the case with some mammalian species whose signs are transmitted culturally through social learning. Also the set of conceptual categories is larger than the set of expressible semantic categories. This is a reasonable assumption if we think of experiments on chimpanzees, showing a rich mental life (some form of theory of mind, some level of conceptualization, understanding of social relationships and hierarchies, some motivation in sharing information, the necessary amount of variability) but a limited capacity to communicate it.

At this hypothetical stage innovation in the communication/linguistic system come across the population: this presupposes a certain group structure with interactions among individuals. Cultural innovations (Reader and Laland, 2003) can have emerged in different contexts present in the evolutionary history of genus *Homo*, such as social play among offsprings, mother and offspring interactions, cooperative needs among group mates: a plausible promising realistic scenario will be described further in details in chapter one (Suman and Pievani, 2015; see also the Self-Domestication Hypothesis, Gibbons, 2014). Innovations are more likely to be understood by closely related individuals and this factor probably played a role also in the evolution of more sophisticated forms of communication as different models based on kin selection argue (Fitch, 2004; 2007; Falk, 2009; Fogarty *et al.*, 2011).

Once the innovation is acquired by a few members of the community it may spread across the population, through different modalities and depending on several factors (Reader and Laland, 2003; Hoppitt and Laland, 2013), being frequency dependent selection one of the most fundamental criteria (we will discuss it in chapter three, Suman, submitted). Through a process of cultural evolution the innovation can get conventionalized, depending on its adaptive value, as a tool of social communication.

At this point, we should clarify to which extent genetic assimilation can occur. Dor and Jablonka (2000) argue in favor of a linguistically-driven genetic assimilation, that is a genetic assimilation occurring after a long period of consistent directional cultural evolution. A complete genetic assimilation will lead in principle towards the genetic fixation of a specific adaptation, a sort of genetic/developmental module for language. However, Dor and Jablonka argue in favor of a *partial genetic assimilation* resulting in a cognition biased towards specific semantic categories, that is a cognition more prone to language acquisition and usage. A partial rather than a complete assimilation is also more compatible with cultural change which remains at high rates and relies deeply on phenotypic plasticity and behavioral flexibility.

Dor and Jablonka's argument hence claims that a certain genetic endowment dedicated to language has to be found. However, it is important to understand the nature of this genetic endowment.

Despite the early enthusiasm that followed the discovery of FOXP2 led to mistakenly present it as the gene for language, today it is widely acknowledged that things are much more nuanced than that. The very notion of a “gene for” is an oversimplification resulting in a flawed conception of biological networks. However, the notion of language genetics in not itself flawed or an illegitimate enterprise. On the contrary it represents a fundamental brick of language evolution studies; researchers should only worry of not adopting a naïve evolutionist view, assigning too much explanatory power to natural selection acting on genes. Studies reviewed in Ramus and Fisher (2009) suggest that many genes affecting cognition are “generalist genes”, producing their effects relatively uniformly in the brain, hence genes that perform several different functions in various organs and stages of development, rather than genes for a specific monofunctional task. Genes associated with dyslexia and other language disorders are turning out to show similar characteristics. Widening our knowledge on the genetic and epigenetic network at the basis of language is crucial for future research, and this is what the Biolinguistics group in Barcelona is aiming at (Boeckx and Benitez Burraco, 2014; Boeckx *et al.*, 2016).

9. A comparison: the moving target argument and the assimilate-stretch principle

The “assimilate stretch principle” by Dor and Jablonka and the “moving target” argument by Christiansen and Chater both conceive an interaction between biological and cultural evolution but with some crucial differences.

Christiansen and Chater conclude that biological and cultural evolution rates of change stand on incompatible time scales, so that it is highly implausible that cultural traits would get fixed in the genetic endowment resulting in task-specific adaptations or a domain-specific innate cognitive device such as UG. They argue instead that language acquisition stands on domain-general cognitive capacities evolved through biological evolution and that cultural evolution set new demanding tasks that allowed pre-existing congnitive biases to get recruited for linguistic use. We will label, in chapter three, this juxtaposition between biological and cultural evolution a *separationist* perspective, as the latter seems to starts where the former stops, and such a perspective finds similarities with the language-ready brain as used by Arbib (2012) (see Suman, submitted). Crucially, Christiansen and Chater assume that the incompatibility between biological and cultural rates of change is due to selective pressures not remaining constant enough.

Dor and Jablonka's model instead assumes the consistency of the selective pressures as a key factor for genetic assimilation of cultural traits to occur. However, they argue this assimilation is unlikely to be complete resulting in a task-specific adaptation or a domain-specific cognitive device such as UG; it will be most probably a partial genetic assimilation of the learned behavior, which allows to free more space for learning and allowing the gradual sophistication of the behavior and its spread through social learning and its cultural evolution. This perspective on the interactions between biological and cultural evolution conceives an integration (*integrative* perspective, see chapter three, Suman, submitted) between the two processes, influencing each other and going side by side.

We believe that in order to understand the kind of interaction between cultural and biological evolution it is crucial to linger on the nature of the selective pressures that might have been involved in language evolution. This focus involves a significant and usually underappreciated shift in the theoretical approach adopted to tackle these questions. We will introduce here some considerations at the basis of the Evolutionary Extended Synthesis proposal. It is crucial to have the best possible understanding of the selective pressures that acted during the long course of human evolution, in order to evaluate their consistency and continuity. We will argue that continuous selective pressures were present in human evolution, and specifically those pressures generated by the systematic modification of the environment caused by niche construction activity.

10. Gene-culture co-evolution and the Extended Evolutionary Synthesis logic

In conclusion of their influential paper, Hauser, Chomsky and Fitch (2002: 1579) suggested that "particular selective pressures, unique to our evolutionary past" may have led, as a direct consequence or as a by-product, to a neural reorganization from which novel cognitive functions might have emerged, being available to be coopted for different tasks, including language faculties.

Szamado and Szathmary (2006) consider why the transition to language occurred only in humans among primates. A transition can be *variation-limited* "when the available genetic variation in the given lineage does not offer even a partial solution to the problem at hand, and it takes a considerable time (in evolutionary terms) for the necessary variation to arise. By contrast, a transition is *selection-limited* if the necessary genetic prerequisites of a possible transition are present, but the given transition is not selected for as this would require a specific ecological or social context" (Szamado and Szathmary, 2006, p. 555).

For example, the transition from the prokaryotic to the eukaryotic cell is better interpreted as a variation-limited transition. Chimpanzees and humans share almost 99% of their genome; some great apes are capable of learning up to some hundreds of lexical items (lexigrams) and partially communicating with sign language, showing also some understanding of novel sentences (Savage-Rambaugh, 1998). Today, researchers argue that chimpanzees possess to a certain degree a theory of mind, a crucial feature for the pragmatics involved in language (Call and Tomasello, 2008).

Simplifying, it can be said that chimpanzees have a rich mental activity, witnessed by their understanding capacities, but a much poorer capacity to express such an activity.

Despite some variation limitation such as the cortico-ambigual connections associated to vocal learning in humans (see Fitch, 2011), Szamado and Szathmary argue that the transition towards human language from primate cognition and communication was primarily a selection-limited transition, "given that no other primates have yet evolved a language-like communication system despite the fact that, arguably, they have the basic cognitive skills required and a similar genetic background to humans" (Szamado and Szathmary, 2006, p. 556).

Laland (2015) argues that selective pressures are usually considered the starting point of standard evolutionary analysis or Standard Evolutionary Theory (SET): a single trait is isolated and the selective pressures promoting the trait are treated as the ultimate causes for the spread and the evolution of that trait. We previously characterized this approach as "atomistic" referred to the isolation of the trait and "externalist" and "unidirectional" as referred to selective causality: the selective environment operating on a trait is the only (ultimate) cause for its evolution. This approach showed limitations as characterized by naive adaptationism and genocentrism (Gould and Lewontin 1979); the researches gathered and described so far put in light the need for a more pluralist and integrative approach. If language transition is characterized as a selection-limited variation, taking selective pressures as the starting point seems a rather limited approach. Instead, what should be asked is where do selective pressures come from, what characterized the selective regime that made that transition possible.

We will argue in this work that niche construction, hence organismal activity, plays a fundamental and underappreciated role in such a transition. We will also argue that a rethinking of the classical distinction between proximate and ultimate causes (Mayr, 1961; Tinbergen, 1963) is necessary to frame the causal elements at the bases of language evolution in order to understand the evolutionary processes involved in language emergence. *Niche construction* theory (Odling Smee *et al.*, 2003) and the concept of *reciprocal causation* (Laland et al., 2011; see also Laland et al, 2013; Laland et al. 2015) give the additional theoretical contribution that allows to frame causality in evolutionary biology in a different way. We will argue (Suman, submitted) that in particular cultural transmission is the additional element that must be taken into account to understand the causal links between selective pressures, the evolved mechanisms and the conditions that allow selective pressures for language to ensue. Chapter three tries to discuss these issues: if we intend language as a selection-limited transition, we argue that in order to understand this transition, a rethinking of the causal relationships among proximate mechanisms, cultural transmission and ultimate causes is needed, and the concept of reciprocal causation provides the proper guidelines for such a rethinking.

The reasons why the theoretical framework proposed by the EES could result the proper theoretical framework within which the evolution of language studies should operate are presented along all the papers gathered in this work: chapter one (Suman and Pievani, 2015), chapter two (Suman, 2016) and chapter three (Suman, submitted).

Exploring the complex intertwine between biological and cultural evolution is the key to understand the processes at the bases of language evolution. We argue that co-evolutionary dynamics between genes and culture were dominant throughout all the evolution of genus *Homo* and deeply characterized hominin evolution.

In particular, evolved cultural traits modified the selective pressures for novel traits and got fixed in a positive feedback process: the more individuals relied on a certain behavior, the more possessing a refined variant of this behavior would result advantageous; in terms of learning and communication, the more individuals learned about the world, the more they could communicate about; and the more they could communicate, the more they could learn. This in principle might generate consistent selective pressures for certain traits or behaviors and it also might speed up the evolutionary rate in a run-away process.

In such a scenario, the cultural evolution of the trait becomes a relevant active causal factor, continuously constructing the selective regime for its own spread. We argue in favor of such a perspective in chapter three.

11. One long argument for the evolution of language: the cultural drive hypothesis

We will argue in chapter three that a gene-culture co-evolutionary dynamic has been in place at least since the appearance of genus *Homo*, representing a deeply influencing evolutionary pattern.

In parallel to development of animal culture studies (Reader and Laland, 2003; Laland and Galef, 2009), researches are revealing more and more that this evolutionary pattern might be much more spread in phylogeny, beyond just humans, than what was previously thought. For instance, a very recent study revealed that the differentiation of populations of Atlantic killer whales has been driven by gene-culture co-evolutionary dynamics (Foote at al., 2016).

We stress again that understanding the evolution of language requires what Darwin would have labeled one long argument, that necessarily has to keep together a large set of evolutionary features: the evolution of the brain, the evolution of cognition, the evolution of cooperation, the evolution of communication, the evolution of culture, just to mention the more macroscopic ones. Multiple factors co-evolved and influenced each others evolution. It seems rather hard to provide a proper evolutionary explanation able to keep together all these heterogeneous topics within a single explanatory framework. However, surprisingly, Kevin Laland in its most recent book *Culturing the mind* (Laland, 2016, in press) provides what seems one long argument for the evolution of human intelligence, cognition and language, presenting it within the guidelines of what we identify in this work as the key concepts of an Extended Evolutionary Synthesis, namely explanatory pluralism, in contrast to the atomistic explanation provided by a naïve evolutionism, and reciprocal causation among several co-evolving features, in contrast to an externalist and unidirectional view of causality represented by the SET view.

We would like to summarize here some of the main points of the hypothesis presented in Laland (2016) and representing the guiding research lines that have driven researches in the Laland Lab in the last years. This analysis starts from the 'cultural drive' hypothesis that was advanced for the first time by Allan Wilson (1934 – 1991). In a nutshell, this hypothesis wants to show how culture drove the evolution of intelligence in primates and in humans.

Allan Wilson noted a correlation between rates at which animals evolve and their brain size, from early amphibians to human beings. In the last 400 million years the brain size of a wide set of vertebrates has increased and accelerated its expansion, suggesting some feedback mechanism at work. Wilson hypothesized the following process: an advantageous habit (innovation) emerges in an individual, it spreads through social learning, selection fixes it, with selection regime established by innovations themselves. Each increment in brain size would enhance the species ability to generate and propagate new habits, in a runaway process. Advantageous habits would favor anatomical evolution, hence, according to Wilson, relative brain size (volume of the brain relative to body size) should correlate to rates of anatomical evolution. Wyles et al. (1983) and Wilson (1985) provided a first confirmation to these data, finding that rates of evolutionary change in body plan correlate strongly with relative brain size in vertebrates.

A fundamental principle of Darwinism is that mutation rate and anatomical evolution rate (number of mutations that get fixed) are independent from each other. However, the latter may be dependent on the rate at which new habits spread, by virtue of the different selective regimes they can generate. Wilson calls it an autocatalytic process mediated by the brain. Today this process has some similarities with niche construction (Odling Smee *et al.* 2003).

Wilson's cultural or behavioral drive hypothesis today is supported by little evidence for mammals and birds. However, this is not the case for the evolution of large brains and complex cognition in primates, hominins and humans (Reader and Laland, 2002; Reader *et al.* 2011; Dean *et al.* 2012; Navarette *et al.* 2016).

We will present here in the Introduction some of the main points of Laland (2016) proposal and we will return to this point in the Conclusions.

12. The evolution of primate intelligence

Reader and Laland (2002) study on animal innovation showed an association between innovation and brain size in primates and birds; they also showed that social learning and innovation co-vary in primates, and that ecologically relevant measures of cognitive abilities were predicted by brain size in primates.

However, some small-brained animals rely on social learning, meaning that they are able to copy others' behaviors; in this sense, invertebrates copying, such as fruitflies, wood crickets or honeybees, seem a challenge to the cultural drive hypothesis, as they don't need big brains.

Simulation experiments such as the social learning strategies tournament (Rendell *et al.* 2010) showed that what was adaptive was not *copying frequency*, but rather *efficient copying*: copying ability rather than frequency brought advantages to their bearers.

So more accurate, more strategic and higher-fidelity copying resulted the most adaptive strategy, which would have ultimately spread through selection. At the same time, functional capabilities and associated structures in the brain will be expected to evolve to the extent they enhance efficient copying and favor innovation.

Better perceptual system like better visual acuity to imitate motor actions (food-processing techniques or tool manufacturing) or better auditory processing and better mapping of sensory inputs to behavioral outputs, connecting visual, auditory, somatosensory and motor cortex are features that are expected to evolve in such a condition. In primates, for example, foraging information is the most socially transmitted knowledge. Effective copying might favor also a theory of mind (ToM) for example in copying facial expressions, or mental time travel (MTT) and planning capacities. Social learning and the spread of cultural transmission would favor higher computation capacities in the brain, decision making, working and long-term memory, mental simulation, features that in humans are associated to the prefrontal cortex, an area particularly expanded in hominin evolution (Deacon, 1997; Somel *et al.*, 2014).

Outside of the brain, at the population level, socially transmitted behaviors such as tool making would easily spread and social tolerance would be favored, particularly among kin; in this sense we explore in chapter one (Suman and Pievani, 2015) the connections with the meaningfulness of the Self-Domestication hypothesis (Gibbons, 2014) in human evolution.

Laland and colleagues' researches around the cultural drive hypothesis touch other fundamental points of cognitive evolution, that will not be reported here in details but just quickly mentioned (see Laland, 2016), regarding the implausibility of a modular cognitive evolution of the primate brain, rather arguing in favor of the evolution of a general intelligence.

Dunbar's Social Brain hypothesis (Dunbar and Shultz, 2007) and its corollary (Social Intelligence hypothesis), according to which primate intelligence has been primarily shaped by selection for social rather than ecological (diet breadth, for instance) or technical (tool use) tasks, is confirmed by several data, but also shows some limitations: for instance, it cannot predict the performance of primates in laboratory tests of cognition (Reader et al. 2011).

A common habit spread through researchers in brain evolution studies was to make claims about the role of a single variable, ranging from diet to group size, to predict brain size and its evolution. The

Social Intelligence hypotheiss is an example that shows the typical structure of what we labeled the SET view, that is isolating a single variable, like group size, and attributing to it the causal primacy for a complex trait such as brain size or primate intelligence. On the contrary Reader and Laland (2011) considered multiple variables at the same time, reaching the conclusion that primate intelligence is characterized by the co-evolution of several factors, shaped both by biological and cultural evolutionary processes (what we labeled here *explanatory pluralism*).

Reader and Laland (2011) made a meta-analysis of published scientific literature, considering more than a hundred primate species and providing quantitative measures of rates of innovation, social learning, tool use, extractive foraging, tactical deception (5 cognitive measures), diet breadth, fruit in the diet and group size (3 social measures), investigating the relations between these measures with statistical methods (principal component analysis, see supplementary material from Reader et al. 2011). "The analysis revealed a single dominant component, which explained over sixty-five per cent of the variance in cognitive measures. (…) Further analyses confirmed that these cognitive abilities were not just correlated in the present, but had evolved together" (Laland, 2016, p. 127). Laland and colleagues conclude that this single dominant component (that they label *factor g*) is a good measure for primate general intelligence, keeping together social, ecological and technical features.

Subsequent studies showed that capuchin monkeys, baboons, macaques and great apes showed convergently evolved high general intelligence; these species are known to deeply rely on social learning (Lewis and Laland, 2012): "this pattern of results is exactly what would be expected if *social learning really were a major driver of the evolution of brain and cognition in primates*. Those primates with high *primate g* scores are those renowned for their complex cognition and rich cultural behavior" (Laland, 2016, p. 129, my italics). Laland concludes that brain size, general intelligence and reliance on culture had co-evolved in primates.

These studies seem to confirm Wilson's original insight, according to whom diverse mental abilities had co-evolved in primates: selection for efficient social learning and innovativeness allowed for energy gains in diet, which in turn fueled brain growth, and generated selection for extended longevity and social learning: "the investment of time in acquiring skill and knowledge leads to selection for lowered mortality rates and greater longevity" (Laland, 2016, p.133). This evolutionary pattern shows surprising similarities with what happened in hominin evolution: we will discuss this point in chapter one and chapter two.

Summing up:

"Group size was not the sole predictor of either brain size or intelligence in our models, and this, combined with our finding that social group size does not predict the absolute size of primate brains, nor the performance of primates in laboratory tests of cognition, reinforced our view that there was more to primate brain evolution than selection for social intelligence. *The most parsimonious way to interpret these findings is to recognize multiple waves of selection for both bigger brains and greater intelligence in primates, operating at different scales.* Our analyses agreed with pre-existing research in recognizing the significance of natural selection for the social intelligence to cope with the complexities of social life, which was probably widespread across monkeys and apes. However, we elaborated on this story, to suggest that selection for social intelligence was followed by a later, more restricted, but nonetheless critical, bout of natural selection favoring cultural intelligence, in a small number of large-brained, social primates, most notably the great apes" (Laland, 2016, p.133-134, my italics)

13. Why only us? The question of cumulative culture

What emerges from these recent studies is that the interaction between biological evolution and cultural traits are much more widespread than just in modern humans. Culture, in animal culture studies, is usually defined as "information capable of affecting individuals' behaviors that they acquire by members of their species through imitation, teaching and other forms of social transmission" (Odling Smee and Laland, 2011). Other vertebrate species and not only primates however rely on dynamics of social learning and cultural transmission, like corivds, parrots, whales and dolphins, and may have faced co-evolution of brain size, general intelligence and reliance on culture. However, language have not evolved in them. Why? Given the autocatalytic nature of the cultural drive process, one species could have run away from the others, but due to which factors? One answer could be pure chance, but it would be scientifically unsatisfactory. Demographic factors instead may have certainly played a role: when population size reached a critical threshold, cultural information was less likely to be lost and knowledge could accumulate.

Mathematical modeling proved to be extremely insightful in inquiring these issues (Enquist et al. 2010; Lewis and Laland, 2012). In fact, another peculiar feature that must be taken into account when dealing with alleged human uniqueness is the human capacity for cumulative culture (Tennie *et al.* 2009), that is the ability to increase cultural traits in diversity and complexity over time. Enquist and colleagues work showed that for a given population size there is a threshold level whereby a small increase in fidelity will transform a cultural trait from being short-lasting to long-lasting. Similarly, Michael Tomasello (see Tennie *et al.* 2009) argued that high fidelity transmission is a critical feature to display the "ratchet effect" of cumulative culture, that is building cultural traits up in diversity and complexity starting from what the previous generation built ("stepping on the shoulders of giants", see Enquist, Ghirlanda, Eriksson, 2011).

Although claims for cumulative culture have been made in chimpanzees (Boesch, 2003) and new caledonian crows (Hunt and Gray 2003), these claims are controversial and to date cumulative culture can be fairly treated as a species-specific human characteristic. Providing a proper definition of cumulative culture is a demanding task that still needs refinement (see Dean *et al.* 2013 and Noël Haidle *et al.* 2015 for a discussion on such a definition).

Lewis and Laland (2012) work quantified innovation, modification, combination, number of traits and trait complexity as factors influencing cumulative culture; they found that loss of cultural traits can be measured and transmission fidelity was shown to be the factor determining trait loss or persistence, hence providing support to Tomasello's argument on the ratchet effect. They also found that combination of traits rather than innovation had a much more relevant impact on cumulativeness.

How have our species reached high fidelity transmission that allowed cumulative culture to ensue? Sticking with Laland and Tomasello's joint hypotheses, through evolving high fidelity transmission mechanisms, a character that would have been subject to positive selection: language is the high-fidelity transmission mechanism evolved by humans, in this perspective.

The refinement of transmission fidelity, given constant selective pressures in this direction, might have represented a long and hard path, starting at least since the appearance of genus *Homo.* Morgan *et al.* (2015) provide an original experimental analysis obtaining data informative for the selective pressures that might have led to the evolution of higher-fidelity transmission mechanisms: a selective gradient for higher-fidelity transmission mechanisms, started with the dawn of cumulative culture in hominins, might have generated the selective environment that led to the emergence of language. We discuss this hypothesis in chapter three. Also, we believe that in this context causal relationships between the factors in play cannot be depicted by the classical distinction between proximate and ultimate causes (Mayr, 1961; Tinbergen, 1963) and we discuss this theoretical argument in chapter three.

14. An updated evolutionary research programme for the evolution of language

We started our work (in the Preface) referring to a theoretical debate on the need of an updating for the evolutionary research programme. We showed in this Introduction how, across the years, many different theoretical approaches have been developed to tackle the thorny issue of the evolution of language. Although we couldn't provide here an exhaustive summary for a too much wide debate, we selected some significant aspects and we identified the core points of a naïve evolutionism that has often been adopted to explain complex interactions. We then highlighted the need of an integration between biological and cultural evolution in order to provide a proper explanation for the origin and the evolution of language. We believe that in the sketch of this ever-ending debate we gave here, we can delineate a shift from a classical SET approach to a EES inclined approach, the latter being in principle able to overcome some theoretical difficulties that were still present with the adoption of a SET approach.

We believe that the cultural drive hypothesis from which Laland (2016) builds up his whole research inquiry can be representative of a EES approach to the evolution of culture, intelligence and language. In the following chapters, conceived as autonomous papers (two of them published, one sumbitted) we will show how the core elements of the EES can be tracked in the evolutionary explanation for the co-evolution of language and cumulative culture we propose in this work. We will add some final considerations in the Conclusions, proposing a tentative expansion of the assimilate-stretch principle by Dor and Jablonka, suggesting it presents some significant continuities with the cultural drive hypothesis. We will also argue that cumulative culture and language should be conceived as two steps of the last major biocultural transition (Maynard Smith and Szathmary, 1995), highlighting also some possible paths for future research.

CHAPTER 1

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The evolution of human language. An alternative scenario

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Abstract

Relying on recent ecological and molecular data coming from hominin branching phylogeny, we develop Deacon (2010) proposal on the role of relaxed selection in the evolution of human language, providing a sound evolutionary background for it, within the human 'Self-Domestication' hypothesis (Gibbons, 2014). We focus in particular on neotenic features of life-history traits and

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brain development, characteristics of modern Homo sapiens, suggesting that they could have spread in an ecological context in which some selective pressures were relaxed. We give an account of how such an ecological condition could have been reached in hominin evolution, relying on the feedback effects of niche construction processes, bringing the case of the use of fire. We provide future possible directions in order to make our hypothesis testable, suggesting it could help solving some issues concerning human evolution and the evolution of language.

Keywords: relaxed selection; neoteny; evolution of language; niche construction; self-domestication; exaptation.

0. Introduction

The role of natural selection has always represented a source of dispute in the language evolution debate, at least since Charles Darwin and Alfred R. Wallace times (Wallace, 1869, 1870; Darwin, 1871; Harris, 1996). A very similar structure of the disputation persists also in the more recent debates, seeing some scholars defending the causal primacy of natural selection in shaping language faculties as adaptive traits, hence selection as a designer (Pinker and Bloom, 1990; Pinker, 1994; Jackendoff, 1999; Pinker and Jackendoff, 2005), and some others relying instead on the role played by structural constraints and functional shifts, hence evolutionary tinkering (Hauser, Chomsky and Fitch, 2002; Okanoya, 2007; Fitch, Huber and Bugnyar, 2010; Fitch, 2010, 2011, 2012).

Within a scientific and naturalistic perspective, it is safely acknowledged that selection has been implicated in the evolution of language faculties. However, the variants of natural selection and the structural and functional traits involved in such a process remain issue of intense debate. Which kinds of selective pressures could have shaped the typically modern human language, if gradually in genus Homo or punctuationally in recent Homo sapiens evolution, is still largely unknown. The debate seems also to suffer from an exaggerated polarization between too confident pan-selectionist and adaptationist approaches, on a side, and a pessimistic skepticism quite indifferent to the most recent evidence, on the opposite side (Pievani, 2015). In the space between, new hypotheses try to account for new, although fragmentary evidence.

In conclusion of their influential paper, Hauser, Chomsky and Fitch suggested that «particular selective pressures, unique to our evolutionary past» (Hauser, Chomsky and Fitch, 2002) may have led, as a direct consequence or as a by-product, to a neural reorganization from which novel cognitive functions might have emerged, being available to be coopted for different tasks, including language faculties. Terrence Deacon (2010) suggested that a relaxed selection may have played a fundamental role in the evolution of language capacity. Relaxed selection on a trait is usually associated to the loss of functionality (Lathi et al., 2009). Hence Deacon's proposal may seem counter-intuitive as it links a decrease of selective pressures to an increase in complexity of a trait.

In this paper we try to answer Hauser, Chomsky anf Fitch suggestion after 13 years of new data and to theoretically develop Deacon's proposal and decline it within a sound evolutionary background, going to investigate which kind of “particular selective pressures” might have acted in the course of human evolution and which kind of effects they might have provoked, taking into account recent data coming from the hominin branching phylogeny.

Deacon's proposal can be synthesized saying, with an analogy, that what could have happened during the evolution of the genus Homo consists in something very similar to what has been observed in a domesticated strain of Lonchuria striata: Bengalese Finches. Let’s begin with this case-study.

1. A model case-study: Bengalese Finches

Bengalese Finches are a domesticated strain of white-rumped munias (Lonchuria striata) which have been domesticated in Japan for over 250 years and artificially bred for plumage. Contrary to the wild individuals, which keep their song simple, Bengalese Finches developed more complex songs which have not been selected for (Okanoya 2004a; 2004b). Deacon 2010 notes that this increase in song complexity, in a remarkably brief period, could have arisen through a global relaxation of selective pressures in the domesticated condition.

Ecological and behavioral studies showed that song variations in wild individuals are due not to genetic distance among populations but to ecological, behavioral and geographic factors (Kagawa et al. 2012; Okanoya, 2012). Wild individuals of Lonchura striata keep their songs simple for three correlated reasons:

1) to avoid predation: a too complex song would be a risky trait in terms of increasing predation rate;

2) to prevent hybridization: white-rumped munias live in sympatry (mixed flocks) with other bird species and varieties, and it has been shown that keeping simple songs has a function in species identification and mate recognition;

3) cost-benefits trade-offs: a too complex song does not seem to be associated to adaptive advantages, thus keeping the songs simple allows white-rumped munias to allocate energies for other tasks.

In Bengalese Finches' domesticated condition these ecological constraints on songs are no longer present: selective predation-related pressures disappear as well as the condition of sympatry with other bird species and varieties. A species-specific bias for simple songs results no longer adaptive in domestication and degenerates rapidly, according to the (negative) expected effects of relaxed selection on a trait (Lathi et al., 2009).

However, the unusual context of relaxed selection allowed Bengalese Finches to experience more complex songs by means of a de-differentiation effect: as constraints on song production are removed or relaxed, other neural systems can be involved in influencing song learning and production (Okanoya, 2004a; Deacon, 2010). Moreover, this tendency towards more complex songs seems to be reinforced by a female preference, that wasn't observed in the wild because absent or masked (Okanoya, 2004a, 2012). Then, after the relaxation of ecological selective pressures, the establishment of novel (sexual) selective pressures has been observed in the novel environmental (domestication) condition.

Deacon's prediction on the (positive, not only negative) effects of relaxed selection on Bengalese Finches seems to be further confirmed by ecological studies (Kagawa et al., 2012). A simulated computational model also showed that a relaxation of selection in a domesticated condition might lead to increasing complexity of song production in Bengalese Finches, even without the female preference (Ritchie & Kirby, 2007).

A suitable way to test Deacon's proposal in the case of human evolution is to frame it within the theoretical approach labeled the “Self-Domestication” hypothesis.

2. The 'Self-Domestication' hypothesis in human evolution

Charles Darwin in The Descent of Man (1871) noted that “man in many respects may be compared with those animals which have long been domesticated”, while in The variation of animals and plants under domestication (1868) he noted a series of characteristics shared by domesticated animals that distinguish them from wild populations. He found that “conditions of living” in domesticated animals led to the appearance of a series of common traits as a by-product of selective breeding for tameness. Such traits include, among others: reduced jaws, flat faces, lower male aggression, reduction of sexual dimorphism and retention of juvenile features and behaviors into adulthood (neotenic traits). The whole set of features exhibited in domesticated condition today has been labeled “Domestication Syndrome” (Wilkins, Wrangham and Fitch, 2014 – see Table 1 for a complete list of traits; see also Hare, Wobber and Wrangham, 2012).

Although the self-domestication of humans is an old suggestion (see Leach, 2003), recent studies have brought new emphasis and novel interesting insights to this topic.

Quite interestingly, it has been proposed by W. Tecumseh Fitch, Richard W. Wrangham and Adam S. Wilkins that a single developmental cause underlies to the apparent phenotypic diversity of the traits exhibited by domesticated mammals: a hypofunction of the cells of the neural crest during early development (Wilkins, Wrangham and Fitch, 2014). It is assumed that animals are primarily artificially selected for tameness; this leads to reduced stress hormone levels, which in turn are responsible for a developmental reduction in neural crest cell input to those tissues associated to the traits of the Domestication Syndrome, as all these tissues are influenced during their development by the neural crest cells. Thus the initial selection for tameness leads, as a non-selected by-product, to the morphological and behavioral characteristics we observe in the Domestication Syndrome (Wilkins, Wrangham and Fitch, 2014).

Here a significant connection with human evolution is emerging. It has been shown that some of the traits of the Domestication Syndrome display a positive trend during the recent human evolution: particularly, a reduction of brow ridges and a shortening of the face (feminization of facial shape) have been shown as a trend over the past 200,000 years, so at least since the appearance of anatomically modern Homo sapiens (Cieri et al., 2014). These morphological features are associated to reduced testosterone levels, reduced male aggressiveness, and reduced sexual dimorphism, as expected in the Domestication Syndrome.

As these craniofacial and skeletal morphologies are pleiotropically correlated to social tolerance, such information could be used to indirectly infer the level of the social bond within the group, as an increase in population density may have corresponded to a demand of increase in social tolerance (Cieri et al., 2014).

At the symposium on 'Domestication and human evolution', held in October 2014 at the Salk Institute of San Diego, California, it has been formally proposed that selection for social tolerance during human evolution led to lower levels of stress hormones (and the associated anatomical features), and favored the spread of pro-social behaviors that distinguished Homo sapiens as a uniquely cooperative species. The hypothesis has been echoed in Science (Gibbons, 2014): in the evolution of early genus Homo individual natural selection may have weakened its effects, leaving room for a stronger selective pressure promoting social tolerance and cooperation. In short, we became more "docile" toward our in-group bandmates, with higher levels of trust and reduced levels of aggression (at least within our group): this constituted a significant advantage in terms of survival and also provided a relatively safer environment to the individual within the group.

We focus now on possible empirical supports to the Self Domestication hypothesis by relying on the role played by relaxed selection and Domestication Syndrome in human evolution. Then we will focus on the candidate surrounding causes for relaxed selection in the evolution of genus Homo.

3. Neotenic features in human brain

A confirmation of the role of relaxed selection comes from human neoteny. As a matter of fact, among the shared traits of the Domestication Syndrome, the neotenic or paedomorphic features, namely the retained juvenile characteristics in adulthood due to a slower developmental rate, deserve a special attention.

Although the idea that neoteny might have played a pivotal role for several reasons in human evolution is an old one (and received recent paleontological confirmations, showing that Homo sapiens reached a peak of neoteny also compared to Neanderthals – Smith et al., 2010), we would like to focus our attention in particular on some neotenic features of human brain development and then reflect on selective aspects that might have characterized human evolution, in order to depict, with an integrated view (inquiring the ecological, behavioral and molecular level – Antón, Potts and Aiello, 2014), an evolutionary scenario for the emergence of those neural structures and cognitive capacities that distinguish today the complex behavior of Homo sapiens and allow this species to make use of articulated language.

In Homo sapiens' peculiar brain development profile (Leigh, 2004; Preuss, 2011; Neubauer and Hublin, 2012), some association areas, related to cognitive functions such as episodic memory, planning, social navigation and learning, are characterized by the presence of neurons that remain structurally immature for the whole duration of their lifespans. Along with an increased expression of genes in these areas and a higher aerobic metabolic rate, these structurally immature neurons lead to a significantly increased synaptic plasticity in adulthood, with important functional and cognitive consequences, such as enhanced learning and mnemonic capacities, which represent fundamental cognitive skills exploited in symbolic culture and language (Bufill, Agustì and Blesa, 2011).

Although specifically human uniqueness, that distinguishes us both from non-human primates and archaic hominins, is getting unveiled more and more, it remains a hard challenge to link it to our peculiar cognitive phenotype. Even if it represents a hard task, skepticism should not take over the whole enterprise (as quite controversially in Hauser et al., 2014). New convergent data are emerging from different fields, from paleontology to molecular biology, to ecology. Among the molecular hallmarks of human brain that might have been involved in the evolution of larger brain size and novel behavioral traits during human evolution (Somel, Liu and Khaiatovich, 2013 – see Box 1),

gene SLIT-ROBO Rho GTPase activating protein 2 (SRGAP2) deserves particular attention.
SRGAP2 is a gene implicated in neocortex development and it is highly conserved among mammals, with the exception of the human lineage where different gene duplications have occurred (Dennis et al., 2012).

It has been shown that SRGAP2:

1) promotes dendritic spine maturation;
2) limits spine density;
3) co-regulates spine density with the length of spine neck (Charrier et al. 2012).

SRGAP2 has undergone at least three duplications in human lineage; the human-specific paralog SRGAP2C is believed to have emerged approximately 2.4 mya, a crucial time in human evolution as it is precisely associated to the expansion of the neocortex, the implementation of first stone tool uses, dramatic changes in behavior, and mostly the divergence of genus Homo from Australopithecus. SRGAP2C is one of the most fixed human-specific duplicate genes as it encodes a functional protein.

It has been shown that SRGAP2C antagonizes the original copy of the gene leading to:

1) a delay in spine maturation, hence neoteny (a heterochrony – see McKinney and McNamara, 1991) during spine maturation;
2) an increased density of spines with longer necks in the neocortex;
3) major consequences in synaptic development and morphology, likely enhancing synaptic plasticity, leading to important implications for cognition, learning and memory (Charrier et al., 2012).

It should be added that gene duplication has been proven to be one of the major sources of evolutionary novelties (Ohno, 1970; Zhang, 2003; Lynch and Katju, 2004). Furthermore some models of gene duplication assign a role to relaxed purifying selection to let the duplicated copies persist and not be deleted (Innan and Kondrashov, 2010 – see Table 1); one copy of the gene shields the other from purifying selection and allows it to accumulate mutations that in a normal regime of selection would be otherwise deleted. In some cases the relaxed selection on the copy, along with the accumulation of modifications, leads that copy to a functional degradation and to a pseudogene status. In other cases the mutated copies might be subsequently coopted for novel functions required by novel selective pressures: this is the well-documented case of the exaptation of hemoglobin, in which some spontaneous duplications expressing different variants were selected in response to different oxygenation demands in early and late fetal development (Hardison, 1999).

The relaxation of selection that is created by the functional redundancy consequent to gene duplication enables what amounts to a random walk away from the gene's antecedent function. But because a random walk produces incremental deviation, there is a significant nonzero probability that one or more of the increasingly variant forms within a population of organisms will “wander” into a related interaction relationship with some duplicate counterpart, and again become subject to selection for any interactive deleterious or synergistic effects. It is no surprise, then, that gene families descended from a common ancestral gene often form synergistic functional complexes. (Deacon, 2010, pp. 4 – 5).

This seems to be the case for the functional synergy observed in the interaction among SRGAP2 and its paralog SRGAP2C, which leads to neoteny in spine maturation, with fundamental implications for synaptic morphology and cognitive functions. Such molecular evidence suggests that neotenic features of human brain development likely played a major role in the evolution of cognition and in the establishment of those cognitive functions that, at a later stage in the evolution of Homo genus, might have been coopted for several functions, including communicative and linguistic faculties.

In the Bengalese Finches case study it has been shown how songs became more complex thanks to a relaxed control over song production and a de-differentiation effect in neural control (Okanoya, 2004a, Deacon, 2010). In human evolution the relaxation of developmental constraints might as well have played a pivotal role. Most interesting and encouraging data in this sense come from a recent study on the transcriptome of human brain and its adaptive role in human cognition (Somel, Rohlfs and Liu, 2014). Here it is shown that heterochronic expression differences in certain areas of the human brain could have enhanced learning and cultural transmission in humans; among the others, SRGAP2 duplication is included. These differences are more accentuated in humans compared with other primates (“human acceleration”, especially in PFC and cerebellum). This «liberal introduction of novel regulatory and coding sequence variants into neurodevelopmental networks and major remodeling of human brain development» (ibid.) constitutes most interesting data that deserve proper explanations. Although finding such explanations represents a forthcoming challenge, one of the three possible paths of inquiry proposed by researchers is the interpretation of such data as evidence of rapid evolution and relaxed constraints on human brain development (Somel, Rohlfs and Liu, 2014). The data are consistent with an evolutionary scenario in which a relaxation of selective pressures allowed a relaxation of developmental constraints which in turn favored the emergence of fundamental cognitive functions.

4. Peculiar hominin life-history traits and selective pressures

We have outlined how a relaxed selection at the gene level, gained through gene duplication processes, could allow functional redundancy to accumulate and become subject of selection at a later stage. We associate now an analogous evolutionary dynamic taking place at the ecological level, in which relaxed selection and neoteny are involved, playing a central role.

Homo sapiens is a species characterized by a peculiar life-history profile, a mixture of both fast and slow components, such as an early weaning but slow somatic growth rate, if compared to wild chimpanzees (Robson and Wood, 2008). Among the peculiar features of human life-history profile, our analysis will focus on slow developmental and growth rate caused by neoteny.

Earlier formulations of the influence of neoteny on human evolution claimed a general shift in human ontogenetic profile in its entirety (Louis Bolk – see Gould, 1977). However, more recent studies showed that this is not the case, as neotenic shifts happened in independent modules of development, suggesting that modern human life-history profile evolved not as a single trait, but rather in a mosaic fashion (Leigh, 2004; Zollikofer and Ponce de Leòn, 2010; Schwartz, 2012; Antón, Potts and Aiello, 2014).

Mosaic evolution is a concept that deals with patterns of evolvability and reflects the idea that an organism does not evolve uniformly as a whole; instead, different parts (or modules), may follow independent evolutionary paths and paces, depending on surrounding selective pressures and constraints. Mosaic evolution is a concept applicable at different levels of the biological hierarchy: a trait (made of several components as the case of a life-history trait, but also like the mammalian brain) may evolve mosaically, meaning that each component of the trait may change independently from other correlated structures (Barton and Harvey, 2000). The transition from a taxon to another, in a geological time scale, may also happen mosaically, with each variety bearing different morphotypes for each homologous trait (Ahlberg and Clack, 2006). This macroevolutionary pattern seems to be relevant for the hominin branching tree (Berger, 2010, 2013), where we see that different species evolve different pathways of change in the elements of functional complexes.

As regards the human brain, heterochronic shifts happened in different areas, suggesting here a mosaic evolutionary pattern of the brain in hominin lineage. In this sense, meaningful studies have been performed on the gene regulation system (the trascriptome) of the Pre Frontal Cortex (PFC), showing no uniform shift in developmental timing between humans and other primates (Somel et al., 2009).

Hence each life-history trait, characterizing any hominin species, is an extremely complex set of structural and functional features that should be taken into account not as the result of a single or uniform shift in development, but rather as the result of a mosaic evolutionary history and as an intersection of different developmental and growth patterns, such as, for example, shape retardation (paedomorphosis) and changes in relative growth velocity, in different tissues and organs (including the brain) (Penin, Berge and Baylac, 2002).

Assumed this evidence, we take into account a well-known neotenic life-history trait typical of Homo sapiens: a prolonged childhood. Such a trait seems to be the result of a series of independent changes, among which neotenic features of brain development, discussed above, might have been present.

It is widely acknowledged that a prolongation of childhood during hominin evolution might have been an important factor for the emergence of language, as it widened significantly the learning window.

However, from an ecological point of view, a prolonged childhood might have resulted an extremely costly trait in terms of individual natural selection. Despite the dramatic advantages in terms of increased learning capacities and plasticity, neotenic offspring remained immature for a longer period, being exposed to predation and other ecological risks that they could have not coped alone. Paleontological data confirm that occasional predation has been a strong selective pressure on human populations until unexpectedly recent times (“Man the Hunted” - Hart and Sussman, 2009). Fragile and immature puppies are a social cost in a demanding and ever-changing environment. Some buffering effects should have been in place to allow the bearers of these neotenic traits to survive and subsequently spread such traits among the population. An ecological trade-off between advantages and risks, between different selective pressures, has been somehow reached. Natural selection should have acted tolerantly at the individual level; in other terms, natural selection should have been relaxed in the ecology of genus Homo evolution.

A prolonged childhood might have favored mother-infants interactions, arguably favoring social learning, along with vocal experimentations: in fact, an honest exchange of information via vocal contact among kin (mother-infants) might have resulted an adaptive strategy for rearing neotenic offspring. Such a scenario for the evolution of language has been labeled “Mother Tongue” hypothesis (Fitch, 2004; Falk, 2009). Vocal calls also represent a costly trait in terms of predation risks, so it seems plausible to argue that a relaxation of selective pressures, at least on the neotenic offspring, might have been a factor playing a decisive role for offspring's survival.

One of the factor that might have contributed to relax selective pressures on neotenic offspring is represented by an enlargement of the social group. In fact, a prolonged childhood might have represented a factor of social cohesion: strengthening the social relationships in small groups in order to protect neotenic offspring could have been one of such balancing adaptive strategies. This irreversibly changed our ecological and social niche and might have strengthened, in turn, a selective pressure in favor of individuals more "docile" and socially "domesticated", particularly males less aggressive towards in-group members and young individuals.

A positive feedback enhanced human self-domestication, resulting in neoteny as an evolutionary trend observed and documented among the several species of the genus Homo (with the maximum in Homo sapiens; Smith et al., 2010). Nevertheless, the initial trigger of such a process of trade-off between antagonistic selective interests is not easy to explain. Other indirect and contextual factors, above the direct cognitive and linguistic implications of a prolonged ontogenetic time for learning and social imitation, could have fostered the ignition of the process, providing to early Homo species a less demanding and severe environment.

5. Relaxed selection at the ecological level as the outcome of niche construction processes: the example of the use of fire

Among the possible causes for relaxed selection in the evolution of genus Homo, the domestication of fire and other cultural innovations are the most important candidates. In order to understand how selective pressures might have relaxed during human evolution, leading to a condition in which costly morphological and behavioral traits as those related to Domestication Syndrome and neoteny could have appeared, it is appropriate to frame human evolution within the theoretical framework of the Niche Construction Theory (Odling-Smee, Laland and Feldman, 2003). Niche constructors are those organisms that, behaving within their ecological niche, with their metabolisms and activities, modify their environment and with it the selective pressures acting on those very organisms. It is a selective bi-directional process. Like other socially complex species, humans are skilled niche constructors, especially thanks to their distinctive cultural capacities (Kendal, Teherani and Odling-Smee, 2011; Sterelny, 2011).

An example of widely niche-performing cultural activity is the control of fire. The use of fire represents a phenomenon, pertaining to the cultural evolution domain, that played a huge role in modifying hominin niche and that elicited not only dramatic behavioral changes, but also structural, anatomical, biological modifications (Wrangham and Carmody, 2010; Atwell., Kovarovic, Kendal Jeremy, in press). Since there is evidence for the opportunistic (and not yet systematic) use of fire, a series of anatomical changes are observable in hominin evolution throughout the fossil record, such as smaller guts, reduced tooth size, reduction of jaws, reduced oral cavity volume, but also increase in cranial capacity.

The control and then domestication of fire constituted also an enormous means of defense against predators, hence it led to a reduction of selective predation-related pressures. Moreover, cooked food led not only to a change of diet, with the intake of more energetic sources through the cooking of vegetables and tubers, but also to a significant reduction in toxin intake, depressing the chance of incurring in mortal diseases. These factors led to an overall reduction of extrinsic mortality rates. Established life-history theory (Medawar, 1952; Williams, 1957) directly correlates the extrinsic mortality rate to longevity and maturation rates. A high extrinsic mortality rate is expected to elicit a life history strategy of the type "live fast, die young", characterized by an early onset of reproduction age; while a reduced extrinsic mortality rate is expected to elicit a life history strategy of the type "live slow, die old", characterized by a slower maturation rate. Although hominin life-history profiles are a mixture of fast and slow components, it is reasonable to assume that a reduced extrinsic mortality rate led to an increase of the lifespan and to a slowdown of maturation rates, with a larger proportion of population surviving until older ages (Wrangham and Carmody, 2010).

We have significant data in this sense, coming from hominin fossil record, at least starting from Homo erectus (Antón, Potts and Aiello, 2014).

From 2.5 to 1.5 mya three lineages of early Homo (H. habilis, H. rudolfensis, H. erectus) evolved in a context of habitat and climatic instability in which larger and taller body size and dietary flexibility resulted as advantageous traits. A trend towards the exhibition of some traits typical of the Domestication Syndrome, such as reduced jaw size, can be found in the known fossil hominins of this period.

Although a systematic use of fire seems to be a quite recent event in human evolution (approximately 350 kya according to Schimelmitz et al., 2014), it has been preceded by a relatively long period of opportunistic use, whose precise dating unfortunately can be unlikely established only by the archeological record. However, biology can offer alternative complementary data, as the study of anatomical data can testify quite reliably a change in dietary habits (Wrangham and Carmody, 2010). H. heidelbergensis differs from H. erectus for larger cranial capacity and many aspects of cranial shape, such as higher forehead, less prognathous face, reduced masticatory strain (Lieberman et al., 2004; Wood and Aiello, 1998). Homo erectus already presents significant differences in this sense compared to late australopithecines, such as smaller mandible, facial shortening, reduced masticatory strain, an expected pattern of reduced gut size, increased energy use such as adaptation to long-distance walking: all features consistent with an enriched diet, probably a cooked diet (Wrangham and Carmody, 2010).

Moreover, there are available data from which we can infer that extrinsic mortality rate was lower in Homo erectus compared to late Australopithecus and probably also to other non-erectus early Homo. From methods of analysis of teeth data (Smith, 2013), we can also infer that developmental rate in Homo erectus was significantly slower than what is known for late Australopithecus, even if very different from the even slower developmental rate shown by Homo sapiens as a peak. Moreover, Homo erectus seemed to be a greater cooperative breeder and a greater cooperative forager than Australopithecus and other early Homo non-erectus. This evidence points in the direction of the presence of enlarged social groups where offspring bearing neotenic features could have been reared in a relatively safer ecological and social context.

Although Cieri et al. 2014 found strong evidence of a trend for the appearance of Domestication Syndrome traits at least since the last 200 kya, such trend could be an older one, starting at least from the appearance of genus Homo around 2.4 mya. The spread of such traits might have been allowed by a relaxation of selective pressures obtained thanks to increasing niche construction activities such as the use of fire.

The Self-Domestication hypothesis, which predicts the appearance of a series of paedomorphic features, (among the others) such as reduction in jaws observed already in Homo erectus, seems to be consistent with a scenario of relaxation of selective pressures.

The interplay between cultural evolution and biological evolution is a topic of growing interest, especially in human evolution (Kendall, Teherani and Odling-Smee, 2011; Fisher and Ridley, 2013; Curry, 2013). Cultural phenomena, produced by biological organisms, can act as feedback factors on those organisms, altering the selective pressures on those very organisms, within a theoretical framework of niche construction. Summing up:

1) The use of fire could have represented an event pertaining to the domain of cultural evolution that operated as a niche modifier and a modifier of selective pressures, mainly leading to a relaxation of selective pressures, provoking dramatic changes not only in behavior but also in biological features.

2) The use of fire can also be intended as a buffer to the potentially dangerous effects implicated in the transition to terrestriality (Wrangham and Carmody, 2010); it can be seen as a “cultural buffer”, capable of producing a cascade of (beneficial) effects at different levels: molecular, developmental, anatomical, functional, behavioral, social, cognitive, ecological.

3) It has to be noted, as highlighted in Atwell, Kovarovic and Kendal Jeremy (in press), that all the possible adaptive responses to a reduction in toxin intake, and more generally to relaxed selective pressures caused by the use of fire, have not been studied exhaustively from an evolutionary perspective yet.

4) The use of fire not only led to a slower maturation rate through a reduction of extrinsic mortality rate, with all the associated changes in life-history and other morphological traits, but it also could have been a factor in eliciting the enlargement of the social group, by means of the diffusion of dramatically novel behavioral habits, probably related to food-sharing strategies. The enlarged social group might have been a relatively secure environment where to rear neotenic offspring, remaining immature for longer periods; in fact, an enlarged social group represented a rich environment to enhance social learning capacities (Pievani, 2011).

5) Moreover, taking care of the immature young kin might have represented a factor of cohesion for the social group, involving in this task also the mature older kin. This classical hypothesis has been labeled the “Grandmother hypothesis” (Hawkes et al., 1998, Hawkes, 2003) and it represents a possible explanation (consistent with a phase of relaxed selection) for some of the fast components of the human life-history profile, as it allowed an early weaning and a shorter inter-birth interval.

6. An alternative evolutionary scenario for the evolution of human language

Here we summarize the relaxed selection evolutionary scenario (Fig. 1):

1) Alteration of the ecological niche by means of niche construction activity, intended as an effect of cultural innovations, of which the use of fire is the example outlined above.

2) Relaxation of ecological selective pressures (reduced predation, reduced toxin intake and in general reduced extrinsic mortality rate).

3) As certain selective pressures are relaxed, some traits might undergo either a loss of functionality or rather a structural reorganization, because of relaxed developmental constraints. This allows functional redundancy to accumulate, as selection acts more tolerantly on the appearance of novel structural and functional features; an example is a delay in development, hence neotenic traits, both at the (3a) organismic level (neotenic life-history traits, such as slower maturation and prolonged childhood) and at the (3b) molecular level (gene duplications such as SRGAP2, which leads to neoteny in brain development, with fundamental implications in terms of function and cognition).

4) Such novel costly traits are not selected against as it would happen in a non-modified niche with a non-relaxed regime of selection, rather they persist and then spread thanks to the novel selective pressures established in the new modified niche. We have seen that such novel selective pressures can be represented by the unveiled female preference for complex songs in the case of Bengalese Finches, considered here in § 1; shifting the focus into human evolution, several different novel selective pressures could have acted in favor of enhanced cognitive capacities, once they were

spread thanks to the initial (1) relaxation of selective pressures.

This process is:

1) a feedback process: niche construction activity modifies the ecological niche and leads to a relaxation of selective pressures that allows the emergence of novel (cognitive and behavioral) traits, that in turn may nourish the niche construction activities.

2) a recursive or iterated process: once the loop is completed it starts again, having as novel initial conditions the outcome of the previous just-ended feedback loop.

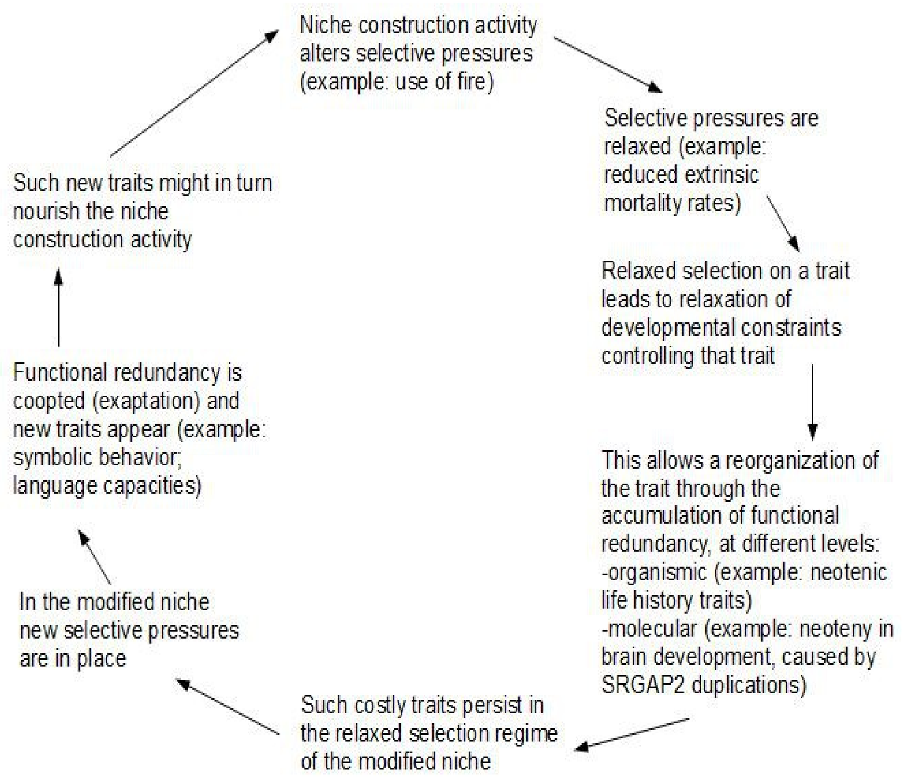

Figure 1. The scheme summarizes the model (a feedback loop), outlined in this paper, for the emergence of costly traits (such as neotenic features) in a regime of relaxed selection: niche construction processes; alteration of the ecological niche; relaxed selection; accumulation first and then cooptation of functional redundancy; appearance of new traits; spread of the new traits through novel selective pressures in the modified niche; such new traits might in turn nourish the niche construction processes. See the text for further details.

Human articulated language could be intended as one of those many behavioral traits, emerged in the long path from the Last Common Human Ancestor (LCA) (which quite surely did not possess it, according to the current data) to Cognitively Modern Humans (CMH). Language (as neoteny above, and as any complex behavior in evolution) should not be reduced to a single evolutionary trait, but conceived as a mosaic of both anatomical and functional interrelated components. For an updated understanding of the evolution of language we should seek not for a single magic feature that would distinguish man from the rest of the animal reign as a Rubicon, but rather for the specific interactions between the several anatomical and functional features implicated in the human language faculties (Okanoya, 2007; Fitch, Huber and Bugnyari, 2010; Fitch, 2012). Each of these features might in principle have had independent evolutionary histories: some very old and gradualistic, while other recent and rapid; and not necessarily linked to single specific functions, being adaptations or exaptations case by case.

In order to properly understand the evolutionary history of such structural and functional features underling the language faculties, we should primarily understand which kind of selective pressures have acted during human evolutionary history. Any evolutionary hypotheses on the emergence of human language should be in close accordance with what we know about overall human evolutionary history and cannot do without it. Then if at least a period of human evolutionary history has been characterized by a relaxation of selective pressures, any evolutionary scenario on the emergence of language must take it into account. By contrast, many past evolutionary stories about human language were based on the speculative adaptationist assumption that a long process of individual natural selection implemented the language performances. Nevertheless, the complexity of the evolution of human traits in hominin phylogeny as we know it today (with more than ten species, the mosaic evolution of crucial traits, strong and persisting ecological instability) makes very difficult to identify a persisting and linear selective pressure (communication skills in hunting, stone tool production, social binding, or sexual selection) able to produce such an effect.

If a relaxation of selective pressures during human evolution allowed the emergence and the spread of important anatomical and functional features (for example neotenic features, at different levels) that reorganized neural structure, enhanced cognitive capacities, which at a later stage have been coopted also for language faculties, we suggest that this evolutionary scenario should be considered an alternative one for the emergence of language (Szamado and Szathmary, 2006).

It represents an alternative evolutionary scenario because the general logic underling the usual selective scenarios is overturned. Usual selective scenarios for the emergence of language basically propose strong selective pressures for one single specific function: a specific ecological context (quite hypothetical) is described and the advantages of a specific function is proposed as the main reason why selection would have favored it. A typical example is a hunting context and the advantages brought by a communicative exchange are identified in the coordination of the hunting group (Washburn and Lancaster, 1968; Hewes, 1973). Many of these selective scenarios have been proposed in the last 50 years, but none of them survived as parsimonious once matched with the evidence collected by the convergent data coming from the highly branching phylogenetic tree of the genus Homo. Such scenarios alone, positing only strong selective pressures for communicative skills, revealed themselves insufficient to gain a proper and complete vision of the evolution of language. We argue that something must be added to bridge the gaps of the conception conveyed by such scenarios, which otherwise might look like 'just so stories'.

Relaxed selection evolutionary scenario posits the attention not on the phase in which strong selective pressures favor the spread of communicative (proto)linguistic faculties, but on the phase before that, the one that constitutes the precondition for the establishment, mainly by means of niche construction processes, of novel selective pressures for those faculties.

We argue that, in order to gain a proper and complete vision of the evolution of language, this issue should be framed in a two-phases process. It is clear, in fact, that relaxed selection cannot do it all alone. In the case of the emergence of complex songs in Bengalese Finches, the process is split in two phases:

1) the first phase consists in establishing a novel environmental context in which selective pressures are relaxed (the domestication condition – even if here it is not reached by niche construction activity), so constraints controlling songs are relaxed, and a neural reorganization of the trait is in place;

2) the second phase consists in establishing novel selective pressures (female preference for complex songs, in this case) that allow the emergence and fixation of the new trait.

The evolution of human language, according to the analysis outlined here, can be split in two phases as well:

1) a first phase in which selective pressures are relaxed through niche construction activities, affecting both behavioral and physiological traits, along with a modification of the environment.

2) a second phase in which the new traits emerge, as adaptations or as functional cooptations (exaptations) of extant structures, in the modified environment, by means of the novel established selective pressures.

As regards the first phase, a possible evolutionary scenario in which selective pressures have been relaxed by means of niche construction activities, allowing functional redundancy to arise, was outlined in this paper.

As regards the second phase, in which novel selective pressures act on or coopt the arisen functional redundancy, many different explanations can be provided to give an account of the spread of language. The previously proposed selective scenarios (Szamado and Szathmary, 2006) should not necessarily be discarded a priori, although it is essential that each of them undergoes a careful matching with the collected interdisciplinary data coming from the hominin evolutionary history, avoiding pan-selectionist shortcuts.

In our discussion, we argued that the 'Mother tongue' hypothesis (Fitch, 2004; Falk, 2009) and the 'Grandmother hypothesis' (Hawkes et al., 1998, Hawkes, 2003) seem consistent with the 'Self-domestication' hypothesis (Wilkins, Wrangham and Fitch, 2014, Gibbons, 2014), a scenario in which the social group expands, the population density within the group increases, favoring the emergence of higher rates of social tolerance among bandmates. Such a context could have provided a safer environment where to rear neotenic offspring, bearers of those neotenic traits which revealed pivotal for our evolution; moreover, vocal exchange of honest information among kin might have resulted an advantageous strategy posing the bases for the evolution of language in such a novel social and ecological context (Fitch, 2004; Falk, 2009).

However, the present work does not intend to provide a final word on how such an evolutionary scenario should be built and much more future analysis is required to supplement what we labeled the second phase of this picture. We do not exclude the possibility that relaxed selection might have played a central role, allowing a fundamental reshaping of the vocal tract, which was later coopted for vocal communication (see below, § 7.2).

7. Discussion and future directions

An evolutionary scenario based on relaxed selection highlights issues that can result of major interest not only for the long standing evolution of language debate, but also in terms of philosophy of evolutionary biology.

1) We argued that neotenic features show an evolutionary trend in the evolution of genus Homo (with a peak in Homo sapiens) due to an active role of relaxed selection.

This perspective challenges the adaptationist logic, which assigns primary agency to classical natural selection and sees developmental constraints only as limiting factors to the power of natural selection in shaping morphologies and behaviours of individuals. This represents the classical view of the evolutionary theory at the time of the Modern Synthesis; however, such conception could result rather limiting. The convergent data brought here suggest that natural selection itself can represent a constraining factor in evolution, while the modulation of developmental constraints can represent a source of evolutionary novelties.

As reported above, the case of white-rumped munias showed how an ecological selective pressure for simple song restrained wild individuals from developing more complex songs, while a relaxation of these selective pressures and the corresponding relaxation of constraints on song learning and production allowed Bengalese Finches to lose simple song bias and develop more complex songs, through a de-differentiation effect in neural bases of song learning and production, directly caused by the relaxation of constraints. This is an example of how ecological natural selection could represent a constraining factor in the evolvability of a trait. In human evolution, ecological non-relaxed natural selection might have played a rather similar constraining role, until it was relaxed by means of niche construction activity.

2) Relaxed selection is traditionally associated merely to the loss of functionality of a trait (Lathi et al., 2009); however, in some conditions, acting on factors regulating development, relaxed selection can represent an active element in shaping or generating novel traits and novel functions.

For example, future researches could verify if reduced jaws in human evolution might be interpreted as the result of relaxed selection on a strong masticatory strain, due to a change in dietary habits (along with the control of fire) and the development of stone tools, which replaced the function played by large teeth. Such a remodeling of the trait might have had a cascade of consequences on many other functions related to facial morphology, not least the vocal apparatus implicated in the production of sounds. It would be interesting to revalue the adaptations of the vocal apparatus not in terms of results of positive selective pressures (which of course might have been involved, but only at a later stage), but in terms of outcomes of a selective relaxation on that trait. In this sense, relaxed selection might represent a possible solution to a paradox which the language evolution debate often refers to: a prone-to-language vocal tract should have been already in place in order to let language evolve, but language itself could not have been the reason why this vocal tract was selected for. Using Ian Tattersall's words: «Quite simply, we have no idea what the reasons were for the acquisition of the reconfigured vocal tract, but we know that it must have been in place before it could be exploited for speech production» (Comment to Lieberman, 2007).

A reconfigured vocal tract could be the outcome of a relaxation of selection during human evolution which brought not only to a partial degradation of the tract (reduced jaws), but also to a reorganization of the vocal tract anatomy which have been later engaged for speech production as an exaptation (Pievani and Serrelli, 2011).

3) What represents the most compelling challenge is filling the gaps between evolutionary levels, namely the ecological level and the molecular level. It has to be further proven that a relaxation of ecological selective pressures results in a relaxation of developmental constraints.

Again, studying the models with which a relaxed selection degrades the functions of a trait, leading to a reorganization of that trait, represents a path to be followed (Lathi et al., 2009). The alternative evolutionary scenario discussed here integrates the ecological level, the behavioral level, the molecular level. These are the features required by an exhaustive and updated evolutionary hypothesis (Antón, Potts and Aiello, 2014), able to give a parsimonious explanation to heterogeneous and convergent data coming from different fields.

Such an analysis succeeds in keeping together different levels of analysis. It also takes into account the different levels and units of selection, like the gene level, the organism level and the ecological level (Okasha, 2006), the trade-offs between antagonistic selective pressures, the modulation of the strength of each selective forcing, the feedback loop between selective pressures and niche-construction activities of organisms. These are examples of the complex machinery of selective processes acting on social species. Future researches should explain the interactions between this multifaceted aspect of natural selection.

4) Evidence in favor of a mosaic brain evolution might represent substantial support in favor of relaxed developmental constraints and relaxed selective pressures.

In fact, a mosaic evolution pattern predicts differential and independent evolutionary trajectories for each module. Recent data from brain development studies (Somel, Rohlfs and Liu, 2014) show differential developmental patterns for different areas of human brain, with differential rates of gene expression, and a relaxation on developmental constraints has been proposed as a plausible underling cause.

Relaxed ecological selection might lead to a relaxation of developmental constraints which allow evolutionary experimentation, hence a mosaic evolutionary pattern. It is interesting to note that mosaic evolution is today called, in paleo-anthropology, for the explanation of many crucial phenomena: the morphology of transitional species (like in the case of Australopithecus sediba – Berger, 2010, 2013); the development and evolution of brain areas; the traits related to neoteny; the evolution of language as an integrated set of anatomical, cognitive and behavioral traits (Fitch, 2012). The significance of this pattern must be further investigated.

5) From a macroevolutionary point of view, a mosaic pattern is consistent with the ecological models of the occupation of new niches. At the beginning of any adaptive radiation, multiple evolutionary “experimentations” is expected if a more tolerant selective regime is in progress.

Biogeographical and paleo-ecological data concerning the hominin “bushy” phylogeny (Berger, 2010, 2013) is consistent with such models, in which usually a first period of developmental and phenotypic plasticity is followed by different specializations (Standen, Du and Larsson, 2014).

Mosaic evolution, relaxed selection, adaptive radiation and different bursts of changes are all elements that intertwine consistently in human evolution, according to the recent data we reviewed here. In terms of macroevolutionary surrounding conditions, another line of future researches could be the hypothesis that a model of early plasticity and branching specialization also applies to the evolution of the genus Homo, highlighting new insights for a better understanding of the evolution of human cognitive and linguistic faculties as well.

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References

Ahlberg P. E., Clack J. A. (2006). A firm step from water to land. Nature, 440, 6: 747-749.

Antón S. C., Potts R., Aiello L. C. (2014). Evolution of early Homo: an integrated biological perspective. Science, 344, 1236828. DOI: 10.1126/science.1236828

Atwell L., Kovarovic K., Kendal Jeremy J. R. (in press). Fire in the Plio-Pleistocene: the functions of hominin fire use, and the mechanistic, develpomental and evolutionary consequences. JASs, 98, 2015.

Barton R. B., Harvey P. H. (2000). Mosaic evolution of brain structure in mammals. Nature, 405, 1055-1058.

Berger L. R., de Ruiter D. J., Churchill S. E., Schmid P., Carlson K. J., Dirks P. H. G. M., Kibii J.

M. (2010). Australopithecus sediba: a new species of Homo-like Austhralopith from South Africa. Science, 328, 195-204.

Berger L. (2013). The mosaic nature of Australopithecus sediba. Nature, 340, 163.

Bufill E., Agustì J., Blesa R., (2011). Human neoteny revisited: the case of synaptic plasticity, American Journal of Human Biology. 23, 729-739.

Charrier C., Joshi K., Coutinho-Budd J., Kim J., Lambert N., de Marchena J., Jin W., Vanderhaeghen P., Ghosh A., Sassa T., Polleuxi F. (2012). Inhibition of SRGAP2 function by its human-specific paralogs induces neoteny during spine maturation. Cell, 149, 923-935.

Cieri R. L., Churchill S. E., Franciscus R. G., Tan J., Hare B. (2014). Craniofacial feminization, social tolerance and the origins of behavioral modernity. Current Anthropology, 55, 4: 419-443.

Curry A. (2013). The milk revolution. Nature, 500, 20-22.

Darwin C. (1871). The descent of man and selection in relation to sex. London, John Murray.

Deacon T. W. (2010). Colloquium paper, A role for relaxed selection in the evolution of the language capacity. PNAS, 107, 9000 – 9006.

Dennis M. Y., Nuttle X., Sudmant P. H., Antonacci F., Graves T. A., Nefedov M., Rosenfeld J. A., Sajjdian S., Malig M., Kotkiewicz H., Curry C. J., Shafer S., Shaffer L. G., de Jong P. J., Wilson R. K., Eichleri E. E. (2012), “Evolution of human-specific neural SRGAP2 genes by incomplete segmental duplication”, Cell, 149, 912 – 922.

Falk D. (2009). Finding Our Tongues: Mothers, Infants and the Origin of Language. New York, Basic Books.

Fisher S. E., Ridley M. (2013). Culture, genes, and the human revolution. Science, 340, 929-930.

Fitch W. T. (2004). Kin selection and ‘mother tongues’: a neglected component in language evolution. In: Oller D. K. and Griebel U., éds. Evolution of Communication Systems: A comparative approach. Cambridge, MA, MIT Press, 275-296.

Fitch W. T. (2010). The evolution of language, Cambridge, Cambridge University Press.

Fitch W. T. (2011). The evolution of syntax: an exaptationist perspective. Frontiers in evolutionary neuroscience, 3, 1-12.

Fitch W. T. (2012). Evolutionary Developmental Biology and Human Language Evolution: Constraints on Adaptation. Evolutionary Biology, 39, 613-637.

Fitch W. T., Huber L., Bugnyari T. (2010). Social cognition and the evolution of language: constructing cognitive phylogenies. Neuron Review, 65, 795-814.

Gibbons A. (2014). How we tamed ourselves and became modern – 'self-domestication' turned humans into the cooperative species we are today. Science, 346, 6208: 405-406.

Gould S. J. (1977). Ontogeny and Phylogeny. Cambridge, Harvard University Press.

Hardison R. (1999). The evolution of hemoglobin. American Scientist, 87, 126-137.

Hare B., Wobber V., Wrangham R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. Animal Behaviour, 83, 573-585.

Harris R., ed., (1996). The origin of language. Bristol, Thoemmes Press.

Hart D. L., Sussman R. W. (2009). Man the hunted: primates, predators, and human evolution – expanded edition. Colorado, Westview Press, Boulder.

Hauser D. M., Yang C., Berwick R. C., Tattersall I., Ryan M. J., Watumull J., Chomsky N., Lewontin R. C. (2014). The mistery of language evolution. Frontiers in Psychology, 5, 401: 1-23.

Hawkes K., O'Connell J. F., Blurton Jones N. G., Alvarez H., Charnov E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. PNAS, 95, 1335-1339.

Hawkes K. (2003). Grandmothers and the evolution of human longevity. American journal of human biology. 15, 380-400.

Hewes G. (1973). Primate communication and the gestural origin of language. Current Anthropology, 14, 5-25.

Innan H., Kondrashov F. (2010). The evolution of gene duplications: classifying and distinguishing between models. Nature reviews – Genetics, 11, 97-108.

Jackendoff R. (1999). Possible stages in the evolution of language capacity. Trends in Cognitive Sciences, 3, 7: 272-279.

Joordens J. C. A., d'Errico F., Wesselinghs F. P., Munro S., de Voss J., Walinga J., Ankjærgaard C., Reimann T., Wilbrans J. R., Kuiper K. F., Mucherl H. J., Coqueugniot H., Prie V., Joosten I., van Os B., Schulp A. S., Panuell M., van der Haasl V., Lustenhouwer W., Reijmer J. J., Roebroeks W., (2014). Homo erectus at Trinil in Java used shells for tool production and engraving. Nature, 518: 228-231.

Kagawa H., Yamada H., Lin R., Mizuta T., Hasegawa T., Okanoya K. (2012). Ecological correlates of song complexity in white-rumped munias – the implication of relaxation as a causa for signal variation in birdsong. Interaction Studeis, 13, 2: 263-284.

Kendal J. R., Teherani J. J., Odling-Smee J. (2011). Human niche construction in interdisciplinary focus. Phil. Trans. Roy. Soc. B., 366, 785-792.

Lathi D. C., Johnson N. A., Aije B. C., Otto S. P., Hendry A. P., Blumstein D. T., Coss R. G., Donohue K., Foster S. A. (2009). Relaxed selection in the wild. Trends in Ecology and Evolution, 24, 9: 487496.

Leach H. (2003). Human domestication reconsidered. Current Anthropology, 44, 3: 349-368.

Leigh S. R. (2004). Brain growth, life history and cognition in primate and human evolution. American Journal of Primatology, 62, 139-164.

Lieberman D. E., Krovitz G. E., Yates F. W., Devlin M., Claire M. S. (2004). Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. Journal of Human Evolution, 46, 655-677.

Lieberman P. (2007). The evolution of human speech – its anatomical and neural bases. Current Anthropology, 48, 1: 39-66.

Lynch M., Katju V. (2004). The altered evolutionary trajectories of gene duplicates. Trends in Genetics, 20, 11: 544-549.

Medawar P. B. (1952),. An unsolved problem of biology. London, H. K. Lewis.

McKinney M. L., McNamara K. J. (1991). Heterochrony – the evolution of ontogeny. New York, Springer Science+Business Media.

Neubauer S., Hublin J. J., (2012). The evolution of human brain development. Evolutionary Biology, 38, 568-586.

Odling Smee F. J., Laland K. N., Feldman M. W. (2003). Niche construction – the neglected process in evolution. Princeton and Oxford, Princeton University Press.

Ohno S. (1970). Evolution by gene duplication, Springer – Verlag.

Okanoya K. (2004a). The Bengalese Finch: a window on the behavioral neurobiology of birdsong syntax. Annals NY Acad Sci, 1016, 724-735.

Okanoya, K. (2004b). Song syntax in Bengalese finches: proximate and ultimate analyses. Advances in the Study of Behavior, 34, 297-346.

Okanoya K. (2007). Language evolution and an emergent property. Current Opinion in Neurobiology, 17, 271-276.

Okanoya K. (2012). Behavioural Factors Governing Song Complexity in Bengalese Finches.

International Journal of Comparative Psychology, 25, 44-59.

Okasha S. (2006). Evolution and the levels of selection. Oxford – New York, Oxford University Press.

Penin X., Berge C., Baylac M. (2002). Ontogenetic study of the skull in modern humans and the common chimpanzees: Neotenic hypothesis reconsidered with a tridimensional procrustes analysis. Am J Phys Anthropol, 118, 50-62.

Pievani D. (2011). Altruism as exaptation, and the evolution of human sociality. In: Sussman R. W., Cloninger C. R., éds., Origins of Cooperation and Altruism. New York, Springer: 41 – 61.

Pievani D. (2015). Between skeptics and adaptationists: new prospects for human language evolution. Ciência & Ambiente, 1-16.

Pievani D., Serrelli E. (2011). Exaptation in human evolution: how to test adaptive vs exaptive hypotheses. Journal of Anthropologiacl Sciences, 89, 1-15.

Pinker S., Bloom, P. (1990). Natural language and natural selection. Behavioral and Brain Sciences, 13, 4: 707-784.

Pinker S. (1994), The language instinct, New York, William Morrow and Company.

Pinker S., Jackendoff R. (2005). The faculty of language: what's special about it?. Cognition, 95, 201-236.

Preuss T. M. (2011). The human brain: rewired and running hot. Ann NY Acad Sci, 1225(Suppl 1): E182–E191. doi:10.1111/j.1749-6632.2011.06001.x.

Ritchie G., & Kirby S. (2007). A possible role for selective masking in the evolution of complex, learned communication systems. In: Lyon C., Nehaniv C. L., Cangelosi A., éds., Emergence of communication and language. Berlin, Springer: 387-401.

Robson S. L., Wood B., (2008) Hominin life history: reconstruction and evolution. Journal of

Anatomy, 212, 4: 394-425.

Schimelmitz R., Kuhn S. L., Jelinek A. J., Ronen A., Clark A. E., Weinstein-Evron M., (2014). 'Fire at will': the emergence of habitual fire use 350,000 years ago. Journal of human evolution, 77, 196-203.

Schwartz G. T. (2012). Growth, Development, and Life History throughout the Evolution of Homo", Current Anthropology, 53, S6: S395-S408.

Smith T. M. (2013). Teeth and human life-history evolution. Annu. Rev. Anthropol., 42, 191-208.

Smith, T. M., P. Tafforeauc, D. J. Reid, J. Pouech, V. Lazzari, J. P. Zermeno et al. (2010). Dental evidence for ontogenetic differences between modern humans and Neanderthals. PNAS, 107, 49: 20923-20928.

Somel M., Franz H., Yan Z., Lorenc A., Guo S., Giger T., Kelso J., Nickle B., Dannemann M., Bahn S., Webster M. J., Weickert C. S., Lachmann M., Paabo S., Khaiatovich P. (2009). Transctiptional neoteny in the human brain. PNAS, 106, 14: 5743-5748.

Somel M., Liu X., Khaitovich P. (2013). Human brain evolution: transcrpits, meabolites and their regulators. Nature Reviews Neuroscience, 14, 2: 112-127.

Somel M., Rohlfs R., Liu X. (2014). Transcriptomic insights into human brain evolution: acceleration, neutrality, heterochrony. Curr. Op. Gen. & Dev., 29, 110-119.

Standen E. M., Du T. Y., Larsson H. C. E. (2014). Developmental plasticity and the origin of tetrapods. Nature, 513, 54-58.

Sterelny K. (2011). From hominins to humans: how sapiens became behaviorally modern. Phil. Trans. R. Soc. B., 366, 809-822.

Szamado S., Szathmary E. (2006). Selective scenarios for the emergence of natural language. Trends in Ecology and Evolution, 21, 10: 555-561.

Wallace A. R. (1869). Sir Charles Lyell on geological climates and the origin of species. Quarterly Review, 126, 359-394.

Wallace A. R. (1870). The limits of natural selection as applied to man. In Id. Contributions to the theory of natural selection – A series of essays, London, Macmillan, 2nd Ed.: 332 – 371.

Washburn S. L., Lancaster C. (1968). The evolution of hunting. In: R. B. Lee, De Vore I. éds., Man the hunter, Aldine, 293-303.

Wilkins A. S., Wrangham R. W., Fitch W. T., (2014). The Domestication Syndrome in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics, 197, 3: 795-808.

Williams G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. Evolution, 11, 398-411.

Wood B., Aiello L. C. (1998). Taxonomic and functional implications of mandibular scaling in early hominins. Am J Phys Anthropol, 105, 523-538.

Wrangham R. W., Carmody R. N. (2010). Human adaptation to the control of fire. Evolutionary Anthropology, 19, 5, 187-199.

Zhang J. (2003). Evolution by gene duplication: an update. Trends in Ecology and Evolution, 18, 6: 292-297.

Zollikofer C. P., Ponce de Leòn M. (2010). The evolution of hominin ontogenies. Seminars in cell & developmental biology, 21, 441-452.

CHAPTER 2

Suman F. (2016) An updated evolutionary research programme for the evolution of language. Topoi, doi:10.1007/s11245-016-9419-7

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An updated evolutionary research programme for the evolution of language

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Abstract

Language evolution, intended as an open problem in the evolutionary research programme, will be here analyzed from the theoretical perspective advanced by the supporters of the Extended Evolutionary Synthesis. Four factors (niche construction, inclusive inheritance, phenotypic plasticity, developmental constraints) and two associated concepts (constructive development and reciprocal causation) will be matched with a selection of critical examples concerning genus Homo evolution, relevant for the evolution of language, such as the evolution of hominin life-history traits, the enlargement of the social group, increased cooperation among individuals, behavioral change and innovations (the use of fire), heterochronic modifications leading to increased synaptic plasticity. A particular form of niche construction will be considered (namely counteractive niche construction or cultural mitigation of selection) in a multilevel framework (from the ecological to the molecular level). It will be argued that the four points mentioned above prove to be fundamental explanatory tools to understand how language might have emerged as a result of a gene-culture coevolutionary dynamics.

Keywords: language evolution; Extended Evolutionary Synthesis; gene-culture co-evolution; reciprocal causation; niche construction; self-domestication hypothesis.

1. Introduction

Given the accumulation of a consistent body of researches going beyond population genetics (West-Eberhard 2003; Odling Smee et al. 2003; Jablonka and Lamb 2005; Pigliucci and Müller 2010), the community of evolutionary biologists recently presented a dichotomous debate among the supporters of an Evolutionary Extended Synthesis (EES) and the defenders of a Standard Evolutionary Theory (SET) (Laland et al. 2014). The former state that SET (the product of the Modern Synthesis) is too narrowly focused on genetic inheritance and mechanisms regulating allele frequencies across generations, assigning causal and informational privileges to genes and treating development and heredity as separate phenomena. EES supporters argue for a more constructive view of development (*constructive development*) and evolution, suggesting that four factors in particular should gain more attention in the evolutionary explanation: (i) niche construction, (ii) inclusive inheritance, (iii) phenotypic plasticity, (iv) developmental bias.

On the other side, it is argued that these four factors are already well included in SET: Darwin himself in 1881 published a book dedicated to earthworms altering soil acidity to better fit their environment, a clear case-study of niche construction (Wray et al. 2014). Moreover, according to SET supporters, developmental bias or niche construction do not directly change gene frequencies, hence they should count as proximate causes. On the contrary, EES supporters argue that organism and development are not passive products of selection, rejecting assumptions of unidirectionality in evolutionary causation (*externalism*), stressing the capacity of organisms to systematically bias selective pressures, criticizing the too rigid distinction between proximate and ultimate causes of evolution (on *reciprocal causation* see Laland et al. 2015; see also Laland et al. 2011; Laland et al. 2013; Scott Phillips et al. 2013).

A scientific discipline showing such a debate on its epistemological status proves to be a very healthy one. According to Lakatos' view (Lakatos 1978), the history of science advances through transformation of scientific research programmes, intended as sets of theories, models, concepts and hypotheses delimited by the choices of a community of scientists. Contrarily to scientific paradigms evolving discontinuously through abrupt shifts (Kuhn 1962), scientific research programmes evolve through continuous changes and processes of updating. The current debate between EES and SET supporters is not questioning the validity of the core of the evolutionary research programme: both sides are fully Darwinan. At the same time, the current debate doesn't resemble a competition between alternative research programmes, but rather a dispute on the need for a progressive updating of the common research programme (see Pievani 2011, 2015).

As pointed out by the EES supporters themselves, “the EES entails not only new research directions but also new ways to think about, and interpret, new and *familiar problems* in evolutionary biology" (Laland et al. 2015, p. 6, my italic).

The aim of the current work is trying to apply the core proposals of the EES, and somehow "test" them, on a very old and *familiar* problem, puzzling evolutionists since forever: the evolution of language, which can be considered an *open problem* for the evolutionary research programme.

The evolution of language will be taken as a specific case-study and will be here analyzed through the lenses of the four factors listed above, plus a fifth one: (1) niche construction, (2) inclusive inheritance, (3) phenotypic plasticity, (4) developmental bias, (5) a multilevel or hierarchical framework of analysis. It will be interpreted under the light of the core concepts proposed by the EES supporters, namely *constructive development* and *reciprocal causation*, in order to see whether this theoretical approach can help reaching useful insights.

2. Biology and culture in language evolution

Language is the outcome not only of classical *biological evolution*, but also of another evolutionary process, namely *cultural evolution,* not necessarily sharing the same logic and the same properties of the previous one (Claidière et al. 2014), in the sense that, for example, the former deals with variation and differential survival of biologically inherited traits, while the latter deals with variation and differenatial survival of culturally acquired traits.

Understanding the interactions between these different evolutionary processes is probably the key to understand language evolution. The language faculty is a complex mosaic of traits, resulting from the combination of several subcomponents, some very old and some rather new, evolved along different evolutionary paths and following different paces (Fitch 2012).

While the last-years debate has been dominated by a dispute on the role played by natural selection in shaping the language faculty (Fitch 2010; see also Pievani 2015b) today the picture has been considerably enriched by a series of studies addressing the role that cultural transmission might have played in shaping language (Kirby et al. 2007; Kirby et al. 2008; Scott Phillips and Kirby 2010).

As shown in Scott Phillips and Kirby (2010) – fig. 1, there has been a phase in human evolution in which language, as we know it today, was not present; nonetheless language precursors or "pre-adaptations" were in place. Moreover, hominin species already exhibited a remarkably complex range of behaviors, such as tool manipulation, a complex social structure in a rather wide biogeographic areal, probably some forms of proto-communication (protolanguage), and these complex behaviors were culturally transmitted. This latter aspect, namely the capacity of producing cumulative culture, is one of those peculiar features distinguishing “culture-ready” hominins from other non-human primates and vertebrates (Tennie et al. 2009).

It is precisely from this ecological, behavioral and cognitive background that the evolutionary explanation for language emergence should arise. Understanding this background and the selective pressures that might have acted on it is the main purpose here.

3. Niche construction and inclusive inheritance

Niche constructors are those organisms that, with their behaviors and their metabolisms, alter the environment in which they live and modify selective pressures accordingly: what is transmitted to the next generation is not only the modified gene pool, but also the modified regime of selective pressures (Odling Smee et al. 2003; Odling Smee and Laland, 2011). As other socially complex species, humans are outstanding niche constructors, especially thanks to their highly developed and distinctive cultural capacities (Kendall et al. 2011).

Gene-culture co-evolution is that evolutionary field-study taking in consideration the possibility that cultural practices might have influenced and transformed the selective environment and hence the selective pressures acting on humans and their genetic endowment (Laland et al. 2010). Perturbations on the selective environment by means of cultural activities can be of various kind, leading to different selective outcomes, that could result in both positive and relaxed selective pressures on specific traits. A classical example of positive selection generated by a gene-culture co-evolutionary pattern is represented by the rapid spread of alleles for lactose tolerance in adulthood thanks to the alteration of the environment produced by the spread of cultural practices of dairy farming (Durham 1991; Curry 2013).

However, cultural activities can also act as agents buffering natural selective pressures. Organisms can initiate a change in the environment (*inceptive* niche construction) or rather they can respond to environmental changes with countermeasures buffering the effects of selective pressures; the latter is defined *counteractive* niche construction (Odling Smee et al. 2003; Laland et al. 2010).

Hominin evolution has been characterized by strong climate instability (Potts 2013), which today is considered one of the main factors eliciting genus *Homo* dispersal out of Africa (Parravicini and Pievani 2015). Responding to such an environmental challenge might have represented a major drive for developing counteractive measures. Counteractive niche construction by means of cultural activities, relaxing and buffering the effects of natural selection on genus *Homo* species might have played an underestimated role in human evolution. The most well-known examples of *cultural mitigation of selection* (Laland et al. 2010) during human evolution are clothes manufacturing, the use of fire, building shelters and the extremely recent spread of agriculture and farming.

It is well-established that cultural activities have been dominant after the Neolithic revolution, completely changing the relationship between humans and their environment.

Although gene-culture co-evolutionary models have been successfully applied to study the effects of this environmental reorganization on the human genome (Laland et al. 2010), it is more difficult to establish whether this pattern could extensively apply to deeper times of genus *Homo* evolution, as we lack direct observation of ancient hominin behaviors and exploitable data on their genetic endowment. However, matching heterogeneous sets of data coming from the archeological record, the paleontological fossil record, laboratory analyses on ancient skulls and teeth, it is possible to make inferences over the behavioral traits of those ancient hominins. Today, evidence is gathering indicating that erectines seem to have benefitted strongly from cumulative cultural knowledge (Stringer and Andrews 2005; Antón et al. 2014). Under this perspective evolutionay dynamics at the bases of language emergence can be interpreted as the result of a culture-biology interaction of this kind.

4. A behavioral innovation leading to a cascade of effects

The use of fire can be considered a buffering effect and a niche-modifier for several reasons: it was a means of defense against predators; it elevated the quality of the diet with more energetic cooked food supporting ever demanding brain metabolism; it lowered the risk of mortal disease by intaking less toxines; it altered food-sharing strategies leading to more cohesiveness and enlarging the social group. This picture is consistent with an overall reduction of extrinsic mortality rates, which in turn have profound effects on life-history traits (Medawar 1952; Williams 1957). In particular longer lifespans and slower maturation rates are among the expected patterns (Wrangham and Carmody, 2010).

Compared to other forms of early *Homo*, *Homo erectus* shows significantly lower extrinsic mortality rates, higher quality diet, greater cooperative foraging and greater cooperative breeding, greater developmental plasticity in terms of body composition and slower developmental rates (Antón et al. 2014). This scenario is consistent with the prediction that *Homo erectus* was already capable of benefiting from cumulative cultural knowledge, using it as a significant niche-modifier and a buffer of natural selection (cultural mitigation of selection).

A recent study, however, attributes *Homo erectus'* decreased masticatory and digestive capacities to meat consumption, fulfilling brain metabolic demands, and stone-tool food processing, instead of cooking, which would have come later (Zink and Lieberman 2016).

Moreover, expressions of symbolic behavior consisting of abstract patterns engraved on fresh water shells have been attributed to member of the same species (*H. erectus*), outside Africa 540 kya in Trinil, Java (Joordens et al. 2014). Even if this finding constitutes just an episodic expression of alleged symbolic capabilities, and it is far from proving members of *H. erectus* were capable of something similar to a language, it can nonetheless be considered evidence in favour of the fact that bursts of cultural complexity have been around in the hominin branching phylogeny much before than the appearance of Cognitively Modern Humans (see D'Errico and Stringer, 2011 for the debates related to the emergence of Behavioral Modernity).

This scenario of reshaped life-history patterns just sketched above (see Suman and Pievani, 2015 for a more extensive treatment of this case-study) is extremely relevant to understand the hallmarks of human evolution and the evolution of language. It has been argued that the unique and complex mosaic of life-history traits characterizing humans (among which the evolution of *childhood* plays a fundamental role) might have been a fundamental prerequisite without which the faculty of language could not have emerged (Locke and Bogin 2006; Hublin et al. 2015): according to Locke and Bogin (2006) not only childhood, but also adolescence played a role in the evolution of elaborated vocal behaviors, enhancing fitness and ultimately integrating performative and pragmatic skills with linguistic knowledge in the faculty of language; different selective pressures are responsible for different features. The so called *Mother tongue* hypothesis also takes into account the reorganization of the life-history traits and proposes a kin selection model for the evolution of the semantic communication component of language (intended broadly as referential properties and gradual sophistication of conveyed meanings) in terms of exchange of honest information among kin, with a significant role assigned to alloparenting strategies: altering the organization of the social group produces effects at the behavioral level with consequences on the exchange of information within the members of the group (Fitch 2004; 2007). Such an hypothesis represents a good explanatory model as it is able to take into account heterogeneous sets of data coming from evolutionary anthropology and use them as a solid background to build an evolutionary hypothesis for a specific component of the language faculty, in this case the semantic one.

The use of fire was chosen as a critical example of that cultural exploration (Dor and Jablonka, 2014) and cultural niche construction that allowed hominins to exhibit plastic behaviors that stand at the basis of a culture-prone brain and that shaped their ecological and selective niche. Among the listed consequences, reshaping of the life-history traits, like longer childhood, is a fundamental and necessary substratum to let language emerge through exploratory processes. This is to stress how the evolution of language should be understood not as an abrupt emergence in recent times of human evolution; the roots of this process must rather be traced back in our deep time.

Getting a clear picture of how our life-history pattern came together is a fundamental part of our explanation for the origin and the evolution of language, as life-history trait evolution can be considered one of the main (biological) causes generating several effects at the social level and consequently leading to the several modifications at the behavioral level, generating the conditions, and the necessity, for culturally transmitting novel behaviors (cultural inheritance), increasing the selective pressures on reliable cultural transmission mechanisms. Proximate and ultimate distinction seems difficult to draw here, while a reciprocal causation view provides a better account for causal interaction.

Language represents a high-fidelity information transmission mechanism that could have co-evolved with the complexity of the behaviors that needed to be acquired and transmitted, as recently suggested by a stone-knapping transmission chain experiment by Morgan et. al. (2015): results show that high-fidelity transmission mechanisms, hence verbal teaching, improves performances more than other mechanisms such as observation, imitation/emulation, simple teaching and gestural teaching. Researchers argue that stone tool-making might have generated selective pressures for high-fidelity transmission mechanisms, hence teaching and language (see also Fogarty et al. 2011; Lewis and Laland 2012). Oldowan technology was probably associated to low-fidelity social transmission, while the transition to Acheulean technology probably marked an increase in fidelity transmission, involving a form of (gestural or verbal) protolanguage. This scenario supports a gradual evolution of language in genus *Homo* and assigns a pivotal role to cultural evolution influencing not only cognitive but also genetic evolution, since this pattern could have been in place for more than 2,5 million years (Morgan et al. 2015, see also D'Errico and Banks, 2015).

As complex behaviors emerged gradually thanks to cultural niche construction activity, they were selected and transmitted as functional niche modifiers. What varies and what is inherited is no longer genes alone, but also behaviors and their transmission mechanisms and selection acts on a widened basin of variation. Niche construction theory and its associated view of inclusive inheritance (ecological inheritance and cultural inheritance) are indispensable perspectives in this respect.

Behaviors intended as potent niche modifiers are capable of systematically bias selective pressures. Niche construction advocates and EES supporters argue that Mayr's (however not Darwin's) proximate-ultimate heuristic distinction has today crystallized into a dogma that prevents to appreciate some fundamental evolutionary features (Laland et al. 2011; Laland et al. 2013; see also Scott Phillips et al. 2011). We argue that the need to overcome this too rigid separation between proximate and ultimate causes is urgent if we want to properly understand the plurality of processes at the bases of language evolution, as the latter represents a complex interplay between the behavioral level and the domain of cultural transmission mechanisms on one side, and the biological level and the domain of classical biological evolution on the other side. Many feedback effects operate between these domains and we suggest that *reciprocal causation* (Laland et al. 2015) offers the correct explanatory framework within which to operate in order to understand language evolution.

5. Phenotypic plasticity (behavioral plasticity)

It is reasonable to suggest that behavioral plasticity have been favored by natural selection during genus *Homo* evolution. However, the other side of the coin should be considered as well: the bearers of a prolonged childhood were offspring that remained immature for longer periods, being not self sufficient. Hence slower maturation rates might have been costly traits, and some buffering effects, again, should have been in place in order to let the immature offspring survive, shifting the costs-benefits ratio towards the advantageous side. Defending immature offspring could have been a factor of cohesion for the social group.

Increased cooperation among group members means also increased social learning and a more efficient spread of acquired behaviors through cultural transmission. Language, along with other forms of information transmission such as imitation or teaching, could have ensured high-fidelity transmission of more and more complex behaviors, allowing cultural knowledge to accumulate among individuals and across generations (Fogarty et al. 2011; Lewis and Laland 2012).

These changes both at the individual and at the group level seem to be partially consistent with a hypotheses that have been advanced recently: the self-domestication hypothesis (Gibbons 2014; see also Suman and Pievani 2015).

In order to understand the evolutionary logic of the genetic recruitment (or *exaptation*) occurred in language evolution, we cannot focus exclusively at the genetic level; we should also advance some hypothesis on the selective pressures that might have elicited this recruitment. The Self-Domestication hypothesis provides, in principle, this evolutionary (ecological and social) background: selection for less-aggressive (and more cooperative) behaviors among group mates might have been in place; consequently, some of the morphological traits listed in the

Domestication Syndrome (Wilkins et al. 2014) might have resulted as by-products, and the genes controlling their development have been positively selected accordingly. It is interesting to note that our current understanding of cranial globularization fits well this evolutionary account (Boeckx, Benitez-Burraco, 2014; Benitez-Burraco et al., submitted).

The scenario just outlined seems consistent with a gene-culture co-evolution explanatory model and a reciprocal causation perspective. A first phase of plastic behavioral response to the mutated ecological and social conditions elicits phenotypic accomodation, in which brain neuroplasticity plays a fundamental role (Anderson, 2010). Novel behaviors translate in new niche construction activities and modifications of the (natural and cultural) selective pressures accordingly. This modified regime leads to selection on specific genes. Language, intended as a high-fidelity transmission mechanism, co-evolving with the complexity of behaviors required to face ever-demanding ecological and social challenges, fits in principle this gene-culture co-evolution evolutionary explanatory model (Fisher and Ridley 2013).

6. Developmental bias and constraints (developmental plasticity)

We would like to suggest that building the language phenotype shares also some interesting features with what the EES supporters intend for *constructive development* (Laland et al. 2015).

According to the constructive development perspective developmental processes are intended as "exploratory processes" in the sense that development is an "open-ended" process (see also *weak linkage* in Kirschner and Gerhart, 2010), responding flexibly to internal and external inputs (Laland et al. 2015) with genetic information playing only a part of the whole game and with epigenetics regulating this process. Language is a trait only partially genetically determined as its phenotype is built during infancy and extended ontogeny.

According to the constructive development view, "genetically specified reaction-norm approach is limited, because phenotypic variation results from ontogenetic selective processes, rather than genes, responding to environmental variation." (Laland et. al. 2015). This point is particularly relevant for language, if we consider the exaptive hypothesis for the evolution of complex vocal learning accounting for the difference between humans and non-human primates, labeled in (Fitch 2011) the "Kuypers/Jürgens direct connections hypothesis".

A developmental hypothesis, involving competition during development between an innate call system based in the brainstem, and the cortico-motor system, was put forward by Terrence Deacon: "By Deacon's hypothesis, evolving the kind of direct cortical control over vocalizations typical of humans would *require* a reduction in the innate call system, and perhaps also the innate call repertoire." (Fitch 2011, p. 5).

This perspective includes exactly the kind of ontogenetic selective process in line with the constructive development view. Fine-tuning (and then canalizing) this developmental process might have been crucial in the course of human evolution to evolve complex vocal learning. Moreover, Deacon expressively argues that a reduction in the innate call system would have been required to let the intentional vocalization system "win" this developmental competition. Relaxed developmental constraints can be considered serious candidates for allowing this developmental plasticity (Suman and Pievani 2015; see also Deacon 2010; Somel et al. 2014).

Epigenetic here is of course a big topic, whose relevance has only recently started being appreciated even in language evolution studies. However, this work doesn't aim at such a comprehensiveness and leaves aside this area which would deserve a much more accurate treatment.

Moreover, the brain is an extremely plastic organ, prone to recruit its anatomical components (*neural reuse*, see Anderson 2010) and language is the result of such a massive recruitment (Steels 2011). Determining the role of genetic modifications in language evolution is one of the hardest tasks in this field-study; some defend the "genes-as-followers" perspective (West-Eberhard 2003), some search for the genetic component that triggered language evolution. Most probably, the truth lays in between, in the sense that a co-evolutionary dynamic between genes and the environemtal and selective effects of the phenotypes produced by these genes may result the most proper perspective.

We would like to bring just an example that might bring more clarity to this viewpoint, even though this work doesn't aim at expanding its theoretical character on the genetic field.

In particular, we would like to focus on a specific and well-known mutation of the gene SLIT-ROBO Rho GTPase activating protein 2 -SRGAP2- (whose relevance was more extensively treated in Suman and Pievani 2015), originated by duplication, that got fixed approximately 2.4 mya, a crucial time for human evolution as it is located at the bases of genus *Homo* phylogeny and at the beginning of the encephalization trend. The human-specific paralog SRGAP2C inhibits the original gene whose function is arresting spine maturation in the neocortex (Charrier et al. 2012): this is a case of heterochrony (specifically neoteny), a differential timing in gene expression leading to prolonged spine maturation in the neocortex (hypermorphosis) and leading to longer necks and larger heads, responsible of enhancing synaptic connectivity and implementing synaptic plasticity.

Such a genetic modification most probably played a significant role in increasing general intelligence and synaptic plasticity, bringing plenty of selective advantage. However this is not enough to assess that genes are the prime movers for language evolution.

"The critical role of genetic or epigenetic evolution was to support broad changes to neuronal structure, for example for regulating synaptic growth, synaptic repairing, or brain expansion" (Steels 2011, p. 10). Consistently with this view, SRGAP2C was the example we provided here.

But once these neurobiological foundations were in place, cultural selective pressures (of the kind discussed in Morgan et al. 2015, hence for high-fidelity transmission) imposed by behavioral modifications, could have favored a significant recruitment of neural and cognitive traits, exploiting the underlying evolved brain plasticity and adapting novel features to pre-existing constraints (Deacon 1997; Christiansen and Chater 2008).

This process of recruitment might have deep roots: for example, Putative Precursors of Speech Dynamics (Ghazanfar et al 2012) can be identified in rythmic facial movements of ancestral primates such as lip-smacking (Tramacere and Ferrari, 2016). However, it is hard to establish whether this exaptive process might have be driven by cultural dynamics influencing the action of biological evolution or the other way around. New developments in "animal culture" (Laland and Galef 2009) studies will shed new light on this field.

Once again, a co-evolutionary dynamic, a reciprocal view of biological causality and explanatory pluralism (biological and cultural evolution acting in concert) seem the proper perspective to adopt here.

7. A multilevel hierarchical framework of analysis

Summing up, the perspective we provided so far keeps together the different levels of the biological hierarchy, from the ecological one, down to the molecular one, passing through the individual and the group level. We started taking into account the perturbation at the ecological level caused by a plastic behavioral response to environmental challenges; we considered the altered regime of selective pressures provoked by the use of fire, an example of counteractive niche construction or cultural mitigation of selection. A behavioral innovation, hence a plastic response not preceded by any gene modification, is in principle capable of triggering a cascade of effects both at the molecular level (heterochrony), at the individual level (prolonged childhood, slower developmental rates) and at the group level (self-domestication hypothesis, increased cooperation). Once the neurobiological biological foundations were put in place by biological evolution (genetic and epigenetic), cultural selective pressures for behavioral transmission might have triggered a recruitment process, made possible by the previously selected plastic features, for the emergence of a high-fidelity transmission mechanism, that is language.

A multilevel perspective is here proposed as a metalevel of analysis that keeps together the factors we considered so far (see fig. 1).

The logic of the argument presented here is consistent with a gene-culture co-evolutionary model. In fact, it does not take a genetic mutation to trigger a response to environmental challenges, but a plastic adjustment of the phenotype (a behavioral response) is sufficient to trigger a modification of the selective regime in a niche construction logic. This modified regime of selection can eventually lead to selection of particular genes or metabolic pathways, such as the well-known case of lactase persistence (Curry 2013), the biological adjustment to the use of fire (Wrangham and Carmody 2010), or even FOXP2 human variants, in a population already using a form of communication system requiring high-fidelity and high variety transmission mechanisms (Fisher and Ridley 2013).

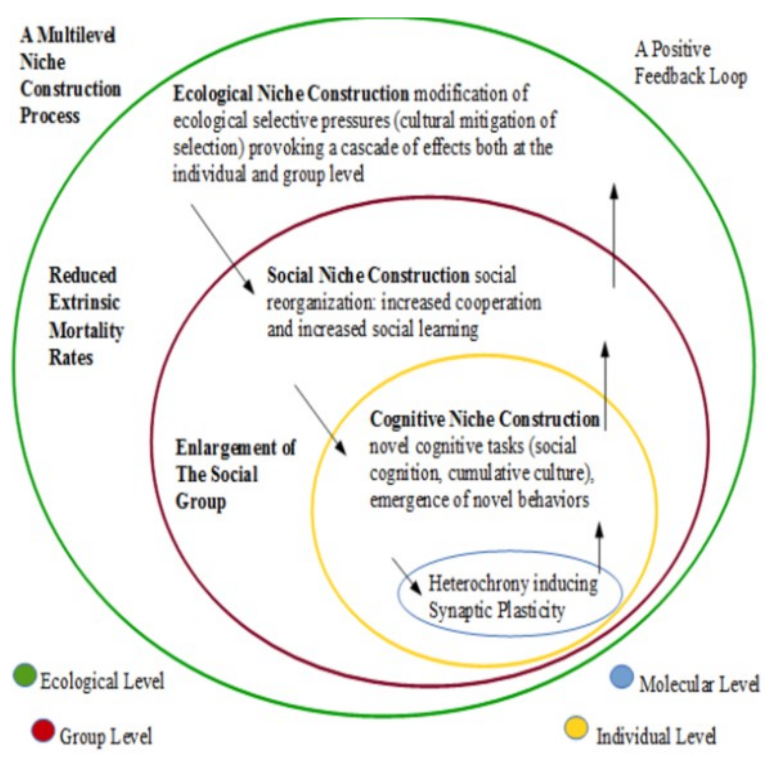

Figure 1. The logic of the gene-culture co-evolutionary dynamic is presented here. A flexible behavioral response to environmental challenges is able to alter the selective regime at the ecological level, provoking a cascade of effects at other levels; alloparenting, increased cooperation, increased social learning are among the modifications occurring at the social level; novel behaviors and mechanisms implementing the transmission of cumulative culture are among the modifications occurring at the individual level; delayed developmental rates caused by heterochronic gene expression are among the modifications occurring at the molecular levels, promoting in turn reliance on social learning and producing positive selective feedback effects.

So if it is fairly accepted that gene-culture co-evolution is a fundamental evolutionary pattern that can explain some recent human genomic adaptations (Laland et al. 2010), we speculate that this pattern can be extended to deeper times in human evolution, not only because cultural and cognitive complexity associated to genus *Homo* species is being unveiled today more and more (Joordens et al. 2014; Rodriguez-Vidal et al. 2014), but also because some hypotheses on the role played by gene-culture co-evolutionary patterns in genus *Homo* evolution have started being inquired experimentally today (Morgan et al. 2015). These recent works however suggest that a thorough reconsideration of the causal roles of the elements in play is needed, namely the interplay between the transmission mechanisms, cultural transmission across individuals and generations and the selective pressures seen from a reciprocal causation perspective.

8. Conclusions

An evo-devo approach to language evolution has surely gained much value in the last years among the scientific community (Dor and Jablonka 2009; Fitch 2012; Boeckx 2014). This work, however, aims at making a further step trying to gather some relevant language evolution studies with the perspective advanced by the EES supporters (Laland et al. 2015). We tried to picture an adaptive complementarity between organisms and their environment throughout genus *Homo* evolution, showing how selective pressures might have changed in accordance to the influence of increasing behavioral complexity.

Conceptual frameworks should be evaluated on their ability to stimulate useful research.

Language evolution can be considered an *open problem* of the evolutionary research programme. Although no novel specific predictions are advanced here, we believe that this conceptual architecture better frames our current understanding of language evolution. Genes, development and the environment *constructively* interact in building the language faculty. Language is the result of a plurality of interactions causally interrelated (*explanatory pluralism*): biological and cultural evolution are complexly intertwined in the evolution of the language faculty, and understanding the interplay of these different systems is pivotal for the future studies on language evolution. We argue that *reciprocal causation* represents a proper theoretical tool to frame the interaction between cultural and biological evolutionary processes as the cultural and social dimension of language have systematically biased selective pressures for language evolution.

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References

Anderson ML (2010) Neural reuse: a fundamental organization principle of the brain. Brain & Behav Sci 33:245-313.

Antón SC, Potts R, Aiello LC (2014) Evolution of early *Homo*: an integrated biological perspective. Science 344:1236828.

Benitez-Burraco A, Theofanopoulou C, Boeckx C (2016) Globularization and domestication. Topoi, DOI: 10.1007/s11245-016-9399-7

Boeckx, C, and Benítez-Burraco, A (2014) The shape of the human language-ready brain. Front Psychol 5:282

Boeckx C (2014) What can an extended Synthesis do for biolinguistics: on the needs and benefits of eco-evo-devo program. In: Pina M, Gontier N (eds) The evolution of social communication in primates, Springer, 313-326

Charrier C, Joshi K, Coutinho-Budd J, Kim J, Lambert N, de Marchena J, Jin W, Vanderhaeghen P, Ghosh A, Sassa T, Polleuxi F (2012) Inhibition of SRGAP2 function by its human-specific paralogs induces neoteny during spine maturation. Cell, 149:923-935

Christiansen MH, Chater N (2008) Language as shaped by the brain. Brain Behav Sci 31:489-558

Claidière N, Scott-Phillips TC, Sperber D (2014) How darwinian is cultural evolution? Phil Trans R Soc B 369:20130368

Curry A (2013) The milk revolution. Nature 500:20-22

Deacon TW (1997) The symbolic species – co-evolution of language and the brain. W. W. Norton & Company Inc., USA.

Deacon TW (2010) A role for relaxed selection in the evolution of the language capacity. Proc Natl Acad Sci 1-7

D'Errico F, Stringer CB (2011) Evolution, revolution or saltation scenario for the emergence of modern cultures? Phil Trans R Soc B (2011) 366:1060–1069

D'Errico F, Banks W (2015) The archeology of teaching: a conceptual framework. Cambridge Archeological journal 25:859-866

Dor D, Jablonka E (2009) Plasticity and canalization in the evolution of linguistic communication: an evolutionary-developmental approach. In: Larson, Richard, Deprez (eds) The evolution of human language, Cambridge University Press, Cambridge

Durham WH (1991) Coevolution. Genes, cultures, and human diversity. Stanford University Press, Stanford, California

Fisher SE, Ridley M (2013) Culture, genes, and the human revolution. Science 340:929-930

Fitch WT (2004). Kin selection and 'mother tongues': a neglected component in language evolution. In: Oller DK and Griebel U (eds) Evolution of Communication Systems: A comparative approach. MA, MIT Press, Cambridge, 275-296

Fitch WT (2007) Evolving meaning: the roles of kin selection, allomothering and parental care in language evolution. In: Lyon C, Nehaniv CL, Cangelosi A (eds) Emergence of communication and language, 29-51, Springer-Verlag, London

Fitch WT (2010) The evolution of language, Cambridge University Press, Cambridge.

Fitch WT (2011). The evolution of syntax: an exaptationist perspective. Front Evol Neurosci 3, 9:1-12.

Fitch WT (2012) Evolutionary Developmental Biology and Human Language Evolution: Constraints on Adaptation. Evolutionary Biology 39:613-637

Fogarty P, Strimling P, Laland KN (2011) The evolution of teaching. Evolution 65, 10:2760-2770.

Ghazanfar AA, Takahashi DY, Mathur N, Fitch WT (2012) Cineradiography of monkey lip-smacking reveals putative precursors of speech dynamics. Curr Biol 22, 3:1176-1182

Gibbons A (2014) How we tamed ourselves and became modern – 'self-domestication' turned humans into the cooperative species we are today. Science 346, 6208:405-406.

Hublin JJ, Neubauer S, Gunz P, (2015) Brain ontogeny and life-history in Pleistocene hominins. Phil Trans R Soc B 370:20140062.

Jablonka E, Lamb MJ (2005) Evolution in four dimensions – genetic, epigenetic, behavioral, and symbolic variation in the history of life. The MIT Press, Cambridge, Massachusetts; London, England.

Joordens JCA, d'Errico F, Wesselingh FP *et al.* (2014) Homo erectus at Trinil on Java used shells for tool production and engraving. Nature 518:228-231.

Kendall JR, Tehrani JJ, Odling Smee J (2011) Human niche construction. Phil Trans R Soc B 366, 1566:783-934.

Kirby S, Dowman M, Griffiths TL (2007) Innateness and culture in the evolution of language. Proc Natl Acad Sci 104, 12:5241-5245

Kirby S, Cornish H, Smith K, (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language, Proc Natl Acad Sci 105, 31:10681-10686.

Kirschner MW, Gerhart JC (2010) Facilitated variation. In Pigliucci M, Müller GB (eds) (2010) Evolution – the extended synthesis. The MIT Press, Cambridge, Massachusetts

Kuhn T (1962) The structure of scientific revolutions. University of Chicago Press, Chicago

Lakatos I (1978) The Methodology of Scientific Research Programmes. Philosophical
Papers, vol. 1, Cambridge University Press, Cambridge (UK)

Laland KN, Galef BG (2009) *The question of animal culture*, Harvard University Press, Cambridge, Mass

Laland KN*,* Odling-Smee J, Myles S (2010) How culture shaped the human genome: bringing genetics and the human sciences together. Nature Rev. Gen. 11:137-148

Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T (2011) Cause and effects in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science 334:1512-1517

Laland KN, Odling-Smee J, Hoppitt W, Uller T (2013) More on how and why: cause and effects in biology revisited. Biol Philos*,* 28:719–745

Laland KN, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J, (2014) Does evolutionary theory need a rethink? Yes, urgently. Nature 514:161–164

Laland KN, Uller T, Feldman MW, Sterelny K, Mu¨ller GB, Moczek A, Jablonka E, Odling-Smee J. (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282:20151019.

Lewis HM, Laland KN (2012) Transmission fideliy is the key to the build-up of cumulative culture. Phil Trans R Soc B 367:2171–2180

Locke J, Bogin B (2006) Language and life history: A new perspective on the development and evolution of human language. Brain Behav Sci 29:259–325

Medawar PB (1952) An unsolved problem of biology. H. K. Lewis, London

Morgan TJH, Uomini NT., Rendell LE, *et al.* (2015) Experimental evidence for the co-evolution of hominin tool-making and language, Nature Communications 6, 6029:1-8.

Odling Smee FJ, Laland KN, Feldman MW (2003) Niche construction – the neglected process in evolution. Princeton University Press, Princeton and Oxford

Odling Smee FJ, Laland KN (2011) Ecological inheritance and cultural inheritance: what they are and how do they differ? Biol. Theory 6:220-230

Parravicini A, Pievani T, (in press) Multi-level human evolution: ecological patterns in hominin phylogeny. Journal of Anthropological Sciences

Pievani T (2011) An evolviong research programme: the structure of evolutionary theory from a lakatosian perspective. In: Fasolo A (ed) The Theory of Evolution and Its Impact. Springer-Verlag, Berlin, 211-228

Pievani T (2015) How to rethink evolutionary theory: a plurality of evolutionary patterns. Evolutionary Biology, DOI 10.1007/s11692-015-9338-3

Pievani T (2015b) Between skeptics and adaptationists: new prospects for human language evolution. Ciência & Ambiente 1-16

Pigliucci M, Müller GB (eds) (2010) Evolution – the extended synthesis. The MIT Press, Cambridge, Massachusetts.

Pitulko et al. (2016) Early human presence in the Arctic: evidence from 45,000 year-old mammoth remains, Science 351, 6270:260-263

Potts R (2013) Hominin evolution in settings of strong environmental variability. Quaternary Science Reviews 73:1-13

Rodriguez-Vidal J, D'Errico F, Giles Pacheco F, et al. (2014) A rock engraving made by Neaderthals in Gibraltar, Proc Natl Acad Sci 11, 37:13301-13306

Scott Phillips TC, Kirby S (2010) Language evolution in the laboratory, Trends in Cognitive Sciences 14:411-417

Scott Phillips TC, Laland KN, Shuker DM, Dickins TE, West SA (2013) The niche construction perspective: a critical appraisal, Evolution 68, 5:1231–1243

Scott Phillips TC, Dickins TE, West SA (2011) Evolutionary theory and the proximate-ultimate distinction in the human behavioral sciences, Perspectives on Psychological Science 6, 1:38–47.

Somel M, Rohlfs R, Liu X (2014) Transcriptomic insights into human brain evolution: acceleration, neutrality, heterochrony, Curr Op Gen & Dev 29:110-119

Steels L (2011) Modelling the cultural evolution of language, Phys Life Rev, doi:10.1016/j.plrev.2011.10.014

Stringer C, Andrews P (2005) The complete world of human evolution. UK: Thames & Hudson. London

Suman F, Pievani T (2015) The evolution of human language: an alternative scenario. Paradigmi Rivista di Critica Filosofica 2:173-196

Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Phil. Trans. R. Soc. B (2009) 364, 2405–2415

Tramacere A, Ferrari PF (2016, in press) Faces in the mirror, from the neuroscience of mimicry to the emergence of mentalizing, J Anthropol Sci

West-Eberhard MJ (2003) Developmental Plasticity and evolution. Oxford University Press, Oxford

Wilkins AS, Wrangham RW, Fitch WT (2014) The Domestication Syndrome in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics 197, 3:795-808

Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. Evolution 11:398-411

Wrangham RW, Carmody RN (2010). Human adaptation to the control of fire. Evol Anthropol 19, 5:187-199

Wray GA, Hoekstra HE, Futuyma DJ, Lenski RE, Mackay TFC, Schluter D, Strassman JE (2014) Does evolutionary theory need a rethink? No, all is well. Nature 514:161–164

Zink KD, Lieberman DE (2016) Impact of meat and Lower Paleolithic food processing techniques on chewing in humans. Nature, 1-9

CHAPTER 3

Suman F. (submitted) Integrative and separationist perspectives: the causal role of cultural transmission in shaping the language-ready brain, Biol & Phil.

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Integrative and separationist perspectives: the causal role of cultural transmission in shaping the language-ready brain

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Abstract

The distinction between proximate and ultimate causes has generated fruitful research but could result rather limiting in certain areas of biology. Biological evolution and cultural evolution are distinct evolutionary processes interacting with each other. Gene-culture co-evolutionary dynamics offer well documented examples of such an interplay. Biological and cultural dynamics are apparent also in human language, where both processes contributed in shaping its evolution. However the nature of this interaction today is still poorly understood. It is often claimed that the emergence of modern language was preceded by the evolution of a language-ready brain: the latter is usually intended as a product of biological evolution, while the former is believed to be the consequence of cultural processes. We label this account as *separationist* and we argue that current evidence coming from the archeological and fossil record suggests that cultural evolution have played a pivotal role in shaping not only modern language but also the language-ready brain. We label here this as an *integrative* perspective. We consequently argue that a rethinking of causation in language evolution is needed when cultural transmission is taken into account. We show the limits of the proximate-ultimate sharp distinction in this specific case-study and we argue in favor of the necessity of a feedback causal model. We extend our argument to the debate on gradual and punctuational evolutionary rates, suggesting that the debate on patterns (gradualism and punctuationism) in language evolution should leave room for discussion on the nature of the processes (separationist and integrative) involved in producing certain patterns, bringing reasons in favor of the integrative perspective.

Keywords: language evolution; cultural transmission; reciprocal causation; gene-culture co-evolution; language-ready brain; processes and patterns; gradualism; punctuationism;

1. Introduction

The proximate-ultimate distinction (Mayr 1961; Tinbergen 1963) represents the standard account for causation in biology. As such it has been adopted also as the core methodology in language evolution studies, generating fruitful research and displaying the explanatory power of the comparative method (Fitch 2005). However, some scholars argued that the proximate-ultimate distinction can sometimes result rather limiting in certain areas of biological inquiry such as evo-devo, niche construction, the evolution of cooperation and language evolution (Laland et al. 2011). Although proximate and ultimate explanations are complementary and not competing explanations, distinguishing proximate and ultimate causes may be not always as straightforward as it might seems. Intersexual selection offers a critical example. Peacock's tail ultimate cause is peahen's choice, that is female mating preference, which is the outcome of proximate (behavioral and developmental) mechanisms; peahen's choice then co-evolves with peacock's tail. In such a perspective, causality is defined as reciprocal rather than unidirectional (natural selection acting on a trait), meaning that a causal feedback loop operates between male and female's traits and generates selection across generations.

This example illustrates how a too rigid proximate-ultimate distinction might sometimes produce a rather unsettling confusion, namely that the causes of phenotypic variation such as behavioral and developmental proximate mechanisms have nothing to do with ultimate, evolutionary explanations (Laland et al. 2011; West Eberhard 2003; Watt 2013).

Language can be addressed as a typical ethological trait, relying on the proximate-ultimate methodology. However, it is clear that a two level distinction is insufficient to frame the processes involved in language evolution; in fact, beyond the phylogenetic level and the ontogenetic level, we have to deal with an additional intermediate level that is the one concerning cultural transmission, often labeled the glossogenetic level (Fitch 2008). Hence, understanding language implies taking into account three different levels of analysis, complexly intertwined, at the same time (Kirby and Huford 2002):

(1) the phylogenetic level: inherited phylogenetic constraints and ultimate causes such as natural selection for specific functions and other neo-Darwinian evolutionary processes involved in language evolution;

(2) the ontogenetic level: proximate mechanisms through which language is acquired such as learning and developmental processes.

(3) the glossogenetic level: languages change over time, but more generally behaviors change over time and they are transmitted across individuals and across generations. Cultural evolution is the evolutionary field-study dealing with how behavioral transmission occurs not only in humans but also in non-human animals relying on social learning strategies (Mesoudi 2011; Whiten et al. 2011). This level is set at an intermediate time-scale between the ontogenetic and the phylogenetic one.

While it is safely acknowledged that natural selection and other neo-Darwinian evolutionary processes are undoubtedly ultimate causes, as well as mechanisms by which language is acquired in ontogeny by each individual are proximate causes, the main point at issue here is whether to consider cultural transmission as a proximate cause (Scott Phillips 2007; Scott Phillips et al. 2011) or rather as an ultimate cause (Laland et al. 2011; Laland et al. 2013) in language evolution and more generally in human evolution. In fact, every hypothesis on the evolution of language should be soundly grounded on the empirical bases available today, that is what we know from the paleontological and archeological record.

Here we present two different perspectives present today in literature providing alternative interpretations, starting from the same empirical phenomena. For conventional reasons of simplicity we label the former stance the “evolutionary psychologist” perspective, endorsing a “Standard Evolutionary Theory” (SET) (Scott Phillips 2007; Scott Phillips et al. 2011); we label the latter the “cultural evolutionist” perspective, endorsing an “Extended Evolutionary Synthesis” (EES) (Laland et al. 2013; Laland et al. 2015; see also Scott Phillips et al. 2013 for such a debate).

2. SET & EES supporters: The evolution of adult lactose tolerance case-study

Researchers supporting the Standard Evolutionary Theory (SET) argue that missing the distinction between proximate and ultimate explanations (Mayr, 1961) is source of epistemic incoherence, confusion, wasted efforts and dangers in language evolution and in cultural evolution studies (Scott Phillips 2007; Scott Phillips et al. 2011): evolutionary psychology (Cosmides, 1989) is quoted as a proper application of the proximate-ultimate distinction which is claimed to be a central pillar of the neo-Darwinian paradigm (see Pievani 2016 for a critique to evolutionary psychology assumptions). Culture is hence usually assimilated to individual learning or environmental effects on behavior, and it is treated as merely a proximate mechanism.

"Evolutionary psychologists often characterize cultural influences on development as operating like a (proximate) switch (like the buttons on a jukebox) to shift behavior and cognition from one pre-established program to another, with each context dependent strategy fashioned by natural selection (Tooby and Cosmides 1992). In contrast, cultural evolutionists view culture as a historical knowledge-gaining process and therefore as a legitimate source of ultimate explanations for acquired human characters (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Mesoudi 2011)" (Laland et al. 2013, p. 724).

Evolutionary psychologists (Tooby and Cosmides, 1992) and SET defenders (Scott Phillips et al. 2011; Dickins and Rahman 2012) usually assume that cultural transmission is genetically controlled, as if cultural change was directly tied to genetic variation in gene-culture co-evolutionary dynamics. Cultural evolutionists instead conceive the phenotype as an open-ended outcome of both evolved developmental processes and learning mechanisms, and so as the interplay between both genetic and cultural inheritance intended as independent but interacting and reciprocally influenced processes (Laland et al. 2010; Mesoudi et al. 2013). EES advocates embrace an inclusive inheritance perspective, arguing that multiple inheritance systems contribute to phenotypic variation across generations (Danchin et al. 2011)

Non-genetic inheritance systems (cultural, ecological, epigenetic inheritance, parental effects) are usually considered in SET as proximate mechanisms evolved as adaptive functions for which natural selection acting upon genetic variation is the ultimate explanation (Dickins and Rahman, 2012). Therefore, non-genetic inheritance systems would not challenge the explanatory structure of SET. Conversely, EES advocates maintain that SET defenders conflate epigenetic inheritance with ontogenetic phenotypic plasticity and cultural transmission inheritance with individual learning (Mesoudi et al. 2013), failing in distinguishing that these mechanisms operate at different time-scales and hierarchical levels.

We lay here as a common ground for comparison a specific case study in which cultural transmission is interpreted differentially by the two alternative perspectives: the evolution of adult lactose tolerance.

Even though all human babies can drink milk, only a few adults have lactose tolerance. It has been shown that the frequency of alleles for adult lactose absorption within a culture correlates with whether that culture has a history of dairy farming. Dairy farming is a cultural practice that spread with the Neolithic revolution, with agriculture, domestication of plants and animals, livestock farming. It started approximately 11 kya in Anatolia and then it spread in Europe (Curry 2013). A typical 'why' question can be asked: why adult lactose absorption has this distribution today? We can see how the two different approaches answer this question.

According to SET supporters (Scott-Phillips et al. 2011; Scott Phillips et al. 2013), the advent of dairy farming changed local ecology; variation in genes for lactose tolerance is correlated with variation in fitness, being natural selection the result of this genetic covariance. Environmental change is not considered as an evolutionary cause, so natural selection acting on genes is the only ultimate evolutionary explanation required. Causality is unidirectional, flowing from the selective environment to the genes carried by the organisms. The spread of dairy farming, a culturally transmitted practice, is flattened to a mere background environmental condition; hence cultural transmission is considered as a proximate cause with no evolutionary relevance. According to a study performed within this conceptual framework (Simoons 1970), genes are the prime movers, that is the spread of lactose absorption alleles allowed dairy farming to spread (Scott Phillips et al. 2013).

According to EES supporters (Laland et al. 2013; Scott Phillips et al. 2013), dairy farming is a culturally transmitted practice that cannot be characterized as caused by earlier selection. That is saying that lactose absorption alleles are not genes for dairy farming at all, they are alleles regulating enzymatic digestion; dairy farming is a complex set of behaviors, knowledge, traditions that are culturally transmitted across generations. As such, dairy farming is considered a niche construction activity (Odling Smee et al. 2003), being able to alter the selective environment, to modify the selective pressures acting within that environment and to trigger the evolutionary event of the spread of lactose absorption alleles. The selective environment and the genetic trait co-evolve in a gene-culture co-evolutionary dynamic (Feldman and Laland 1996). According to a set of researches conducted within this conceptual framework (Feldman and Cavalli-Sforza 1989; Durham 1991; Holden and Mace 1997; Aoki 1986; Gerbault et al. 2011), the spread of dairy farming preceeded the spread of lactose absorption alleles. In such a perspective genes are “followers” (West Eberhard 2003) meaning that a plastic behavioral response to the environment alters the selective pressures and generates the selective regime that favors the spread of the alleles. In this sense, cultural transmission plays an important evolutionary role.

The two accounts just presented reach opposite conclusions on what is the cause and what is the consequence of what. Here we would like to highlight some problems related to the SET view, assigning cultural transmission to the category of proximate mechanisms.

Firstly, proximate mechanisms should operate within the individual lifespan, while cultural transmission, by definition, is transmission of behaviors among individuals and across generations. SET supporters conflate individual learning with cultural transmission, while they are mechanisms operating at different time-scales.

Secondly, by reducing dairy farming to a background environmental condition they do not recognize cultural transmission as an independent system of inheritance, while today it is acknowledged that multiple systems of inheritance contribute to phenotypic variation across generations (Danchin et al. 2011).

Today the interactions between biological and cultural evolutionary processes have been developed in population genetic models by theoretical biologists, showing how deeply selection can be biased by this interaction (Odling Smee et al. 2013). Recent analyses on human genome showed that hundreds of genes might have responded to cultural biases of selection produced by human activities (Laland et al. 2010). Hence, "when an evolutionary mutation is identified as crucial to the human capacity for cumulative culture, this might be a consequence rather than a cause of cultural change. The smallest, most trivial new habit adopted by a hominid species could – if advantageous – have led to selection of genomic variations that sharpened that habit" (Fisher and Ridley 2013, p. 3)

3. Gene-culture co-evolutionary dynamics for language

Current studies in language evolution are putting more and more light on the relevance of a gene-culture co-evolution approach to language (Sterelny 2012; Jablonka et al. 2012; Dor and Jablonka 2014; Morgan et al. 2015). In gene-culture co-evolutionary models, the control of the phenotype is not exclusive matter of genetic determination; cultural transmission mechanisms of learning, phenotypic and behavioral plasticity are also involved (Suman, 2016).

Although biological and cultural evolution are processes operating at different time-scales, they interact with each other. The key point is trying to understand how far back in time this interaction could go and in which ways it is articulated. By doing so we might evaluate the proper causal role of cultural transmission in language evolution, according to empirical evidence in paleoanthropology and archaeology.

Furthermore, understanding the causal role of cultural transmission might result pivotal to advance some predictions in order to bring clarity to the protracted debate on whether language evolved gradually at uniform rates or rather punctuationally, a topic we will discuss in the last paragraph before the conclusions.

According to these debates, we think that three main positions, concerning the processes at the basis of language evolution, can be identified today in literature.

1) a *saltationist* perspective, according to which a genetic mutation, occurred between 100 and 50 kya, triggered language appearance giving the alleged genetic endowment that makes humans unique. (Chomsky, 2010; Berwick et al., 2013; Bohluis et al. 2014). This stance, supporting a lucky mutation being responsible for letting the whole human language package emerging abruptly, without any role for natural selection, is believed to be anti-Darwinian and no longer tenable (Hillert, 2015; Lieberman, 2015; but see Bohluis et al. 2015), hence we won't further discuss it here.

2) a *separationist* perspective: language readiness (see below) was shaped by biological (genetic and epigenetic) evolution; then, approximately 50-100 kya, cultural conditions, often generically defined, allowed the emergence of modern (or true) language. In such a perspective, the causal role of culture enters pretty late the evolutionary scene and is exclusively associated to the emergence of modern "full-developed" language (Christiansen and Chater, 2010; Arbib, 2012; Pagel 2012).

3) an *integrative* perspective: cultural transmission played an evolutionary role not only in the evolution of modern language, but also in previous forms of communication (protolanguages) and it should be considered a causal evolutionary factor in shaping language readiness (Laland 2016, in press; Morgan et al. 2015 and discussion below).

Today, a term used to refer to the biologically evolved capacity to acquire language is *language readiness* or *language-ready brain*. This term stands for the neural features evolved during hominin evolution (not expressively for linguistic functions) and representing the scaffolds that allowed modern language to emerge (Arbib 2012; Boecks and Benitez Burraco 2014). Typically, in this perspective, language readiness is intended as a product of biological (genetic and epigenetic) evolution, while the emergence of modern language is intended as a cultural invention, as a consequence of specific cultural conditions (Kirby et al. 2008; Christiansen and Chater 2008; Christiansen and Chater 2010; Scott-Phillips and Kirby 2010; Arbib 2012; Pagel 2012). In this sense, modern language appearance is usually dated approximately 100 kya, associating it to the explosion of Behavioral Modernity (D'Errico and Banks 2013) observed in the archaeological record.

We label this stance the *separationist* perspective and we believe it presents some problems related to the alleged evolutionary processes that shaped language, in particular regarding the causal role assigned to cultural transmission in hominin evolution.

This separationist account is well depicted by some crucial passages in Arbib's (2012) argument, in the sixth chapter where the core hypotheses of the book are revealed: the hypotheses presented in Arbib (2012) distinguish

> “*biological evolution*, which shaped the genome for a language-ready brain (and body), from *cultural evolution*, which took us from hominids with a language-ready brain and rudimentary manual-vocal communication (protolanguage) to humans with full language capability. I will argue in later chapters that the demands of protolanguage in hominids prior to *Homo sapiens* contributed to the evolution of the human brain, whereas those features that distinguish language from protolanguage did not” (Arbib 2012, p. 162)

And again:

> “It has been the argument of this book that many different changes during *biological evolution* gave humans a *language-ready brain* but that it took *cultural evolution* to exploit the human brain’s capabilities to the point where the potential for language (in the singular) became realized in the development of diverse languages (in the plural) as *Homo sapiens* developed different groupings in Africa and spread from there around the world” (Arbib 2012, p. 251)

Arbib's argument can be summarized as follows: biological evolution built the scaffolds for a language-ready brain, with a central role played by the Mirror System; the scaffolds comprehend: a mirror system for grasping in the common ancestor between monkeys and humans; simple imitation in the common ancestor between humans and ape; complex imitation unique to genus *Homo*; pantomime; multimodal protolanguage (protosign and protospeech). When cultural evolution entered the scene, *true* language (provided with compositional semantics) could emerge in all its diversity and complexity.

The aim of our work is not entering the linguistic, the cognitive and the neural details of Arbib's proposal, which certainly provides promising insights for language evolution studies, but just evaluating the causal role assigned to culture in its account of language evolution.

In the figure 6.2 (Arbib 2012, p. 159) a straight line goes from animal communication systems to protolanguages and biological evolution alone is the process responsible for such a transition. Then the same straight line starts from *Homo sapiens,* it goes towards Indo-European languages and cultural evolution is retained responsible of such a change.

Depicting the evolutionary processes responsible for language evolution as a straight line that shifts from biological to cultural evolution represents exactly what we labeled a *separationist* account.

We argue that there are at least two critical points in Arbib's account:

1) the absence of overlapping between the biological and cultural evolution lines;
2) cultural evolution starting only with *Homo sapiens* appearance.

The same problematic perspective is present in Pagel (2012):

> "language evolved to solve the crisis that began when our species acquired social learning – probably some time around 160 to 200 kya" (Pagel 2012, p. 280)

and in Christiansen and Chater (2010):

> "Instead of viewing the brain as having a genetically specified, domain-specific system for language, which must somehow have arisen over the course of biological evolution, we see the key to language evolution to be evolutionary processes over language itself. Specifically, we view language as an evolving system, and the features of languages as having been shaped by repeated processes of acquisition and transmission across successive generations of language users" (Christiansen and Chater 2010, p. 5)

> "Cultural evolution will work against biological (co)evolution in the case of malleable aspects of culture— rapid cultural change leads to a fast-changing cultural environment, which serves as a "moving target" to which biological adaptation cannot occur" (Christiansen and Chater 2010, p. 12)

Such an account of language evolution poses a sharp separation between biological and cultural evolution, not supported by the updated empirical evidence about hominin phylogeny. We believe that the quoted accounts underestimate the role played by cultural transmission and social learning, as cultural evolution and social learning simply did not enter the evolutionary scene with *Homo* *sapiens*, but instead played a significant role during all the evolution of genus *Homo*.

Each hypothesis on language evolution should be primarily in accordance with the most updated data coming from the archeological and paleontological records. Today, the archeological and the paleoanthropological records coming from hominin branching phylogeny suggest that these two processes have worked side by side (inclusive inheritance and explanatory pluralism perspective, see Suman 2016) at least since the appearance of genus *Homo* (or even before) and so they should be integrated in a gene-culture co-evolutionary interaction in order to understand how uniquely human and interdependent features of cumulative culture and language have emerged.

Here we briefly list some of the main compelling evidence. The first evidence of material culture are today set with the Lomwekian tools 3,3 mya, and tentatively associated to *Kenyanthropus platyops* (Harmand et al 2015). The presence of such a lithic industry indicates that those hominins were already relying on rather advanced social learning practices, hence cultural transmission. Oldowan technology (Semaw *et al.*, 1997), usually associated to *Homo habilis*, appears in the archeological record around 2,4 – 2,6 mya and shows stasis for 700 ky. Acheulean technology (Lepre et al. 2011), usually associated to *Homo erectus*, the first hominin species coming out of Africa, appears 1,7 mya and shows significantly different and novel characteristics, such as bifacial processing. Erectines showed morphological, behavioral and developmental features suggesting that they were benefitting from cumulative cultural knowledge (Antón et al., 2014) and probably they already exhibited a pre-syntactic protolanguage (Tallerman and Gibson 2012).

Moreover, theoretical analysis showed that "individual learning, social learning (from the parental generation), and innate determination of behavior are favored by natural selection when environmental changes occur at short, intermediate, and long generation intervals, respectively" (Aoki et al. 2005, p. 335). Climatic fluctuations indeed played a pivotal role in the evolution of human behavioral flexibility and adaptations (Parravicini and Pievani 2016, in press). Consequently, we could expect that hominin species evolved individual learning as a fundamental adaptive strategy. However, evidence coming from the fossil and archeological record suggest that hominins have relied on complex social interactions at least since the appearance of the first lithic industries, hence Lomekwian, 3,3 mya (Harmand et al. 2015). Climatic fluctuations effects should have been attenuated in order to let hominins evolve social learning adaptive strategies. This consideration support the idea that (cultural) niche construction activities have long been in place in hominin evolution, allowing hominins to build environments in which to fit. Counteractive niche construction (Odling Smee et al. 2003; Laland et al. 2010) is an example of such an evolutionary mechanism favouring hominins fit to their constructed environment. As culture may have been the main factor allowing this environmental modification and eventually human adaptation to a wide range of environments (out of Africa), selection for more and more efficient cultural capacities should have been strong in hominin evolution, especially on those hominin species coming out of Africa, coping with several different environments, from at least two million years ago. Constant selective pressures for cultural variants, allowed human cultures to grow in diversity and complexity, in several human species.

However, culture, in order to be cumulative, requires high-fidelity transmission (Lewis and Laland 2012), and verbal language is such a high-fidelity transimission mechanism. In order to support the transmission of cumulative culture, hominins evolved more and more complex forms of communication along with the increasing complexity of cultural variants in a co-evolutionary dynamic.

Summing up, the archeological and the paleontological records provide strong evidence today in favor of the third stance we labeled the "integrative" perspective, that is a gene-culture co-evolutionary scenario in genus *Homo* evolution. This scenario supports a co-evolutionary dynamic between higher and higher-fidelity transmission mechanisms and culture, and supplementary experimental data seems to support such a prediction (Morgan et al. 2015), as argued below.

4. Causality in co-evolutionary feedback processes: cultural transmission shaped the language-ready brain

Although other non-human animals relying on social learning strategies exhibit cultural variation (Whiten et al. 1999), today there is no available compelling evidence that animal culture is cumulative (although see Boesch 2003). Cumulativeness, that is cultural traits increasing in diversity and complexity over time, seems to be a uniquely human characteristic (Tennie et al. 2009). In order to be cumulative, human culture must be reliably transmitted and language is indeed a high-fidelity transmission mechanism (Lewis and Laland 2012).

A recent study, which we argue being representative of the EES conceptual framework, claims to have found experimental evidence for the co-evolution of hominin stone-tool making and language (Morgan et al. 2015). Other studies previously explored the connections between the putative cognitive capacities required for the stone knapping practice and those exploited in linguistic functions, showing how both tasks could rely on hierarchical planning of actions (Stout 2011; Di Vincenzo and Manzi 2013).

In considering Morgan et al. (2015) experiment, what we want to evaluate is the evolutionary causal role of cultural transmission, and its interplay and overlapping with biological evolution, in the evolution of hominin transmission mechanisms.

184 adult human participants were disposed along chains and tested for their Oldowan tool-making skills under 5 different learning conditions: reverse engineering, imitation/emulation, basic teaching, gestural teaching and verbal teaching. Results showed performances improved under higher-fidelity transmission mechanisms, hence gestural and verbal teaching, the latter involving verbal communication. Researchers argue that stone tool-making might have generated selective pressures for high-fidelity transmission mechanisms, hence teaching and language. Researchers suggest that the evolution of material culture, such as relying on stone-tool making and its social transmission, generated a selective gradient towards high-fidelity transmission mechanisms.

The findings of this study suggest how language might have evolved through gene-culture co-evolutionary dynamics, and more generally they provide a gene-culture co-evolutionary account of human technology and cognition. Even though Oldowan technology probably relied on relatively low-fidelity transmission mechanisms, such as observational learning or simple imitation, social transmission of material culture might nonetheless have generated a continuous selective gradient towards higher-fidelity transmission mechanisms, hence verbal teaching. Later technologies would have reinforced this gene-culture co-evolutionary dynamic.

It is only with more advanced Acheulean and Mousterian lithic technologies that tool-making processing shows long sequences of planned and hierarchically organized actions. The study hence speculates that hominins relying on social transmission of material culture possessed a capacity for teaching and potentially a form of (gestural or verbal) protolanguage around 1.7 mya.

As already mentioned, evidence coming from the archeological and paleoanthropological record support in principle this conclusion (Tallerman and Gibson 2012): cooperative breeding, cooperative foraging, slow developmental rates (Antón et al. 2014) represent indirect evidence that erectines probably benefitted from cumulative cultural knowledge.

Moreover, as Acheulean technology (characterized by bifacially processed amigdala), required hierarchical planning of action in order to be obtained, it has been argued that this skill could represent a precursor of the hierarchical organization and planning of action subsequently employed in linguistic structures (Di Vincenzo and Manzi 2013).

In such a scenario, teaching, a certain form of protolanguage and the associated transmitted cumulative culture, represent potent niche modifiers, being able to systematically bias selective pressures and generate new ones. In such a perspective, protolanguage and language might have evolved following a gene-culture co-evolutionary dynamic in parallel with the evolution of cumulative culture.

What is crucial to recognize in such a co-evolutionary dynamic are the feedback effects between (1) the transmission mechanisms and (2) the selective gradient acting upon them generated by (3) the cultural transmission, nourished in turn by (1) those very transmission mechanisms. Let's try to decompose this feedback causal relationship in its components:

1) transmission mechanisms: imitation, teaching, language can be intended as proximate mechanisms (developmental and neural mechanisms are not directly addressed here, the cognitive and neural level are black-boxed).
2) the selective gradient for high-fidelity transmission mechanisms can be intended as an ultimate cause for the evolution of transmission mechanisms.
3) Social learning among individuals and cultural transmission among generations can be intended as the triggering factor for the selective gradient.

Acknowledging the causal role played by cultural transmission in this co-evolutionary feedback process is crucial. The SET approach typically doesn't ask where do these selective pressures come from. The selective pressures are instead usually considered the starting point of evolutionary analysis in SET approach. Moreover, "the convention within evolutionary biology is to distinguish evolutionary processes from the causes or modulators of those processes" (Laland 2015). However, this convention can be questioned. A simple intuitive example brings clarity to this point:
"if a nail is hit with a hammer we describe the hammer as the direct cause of the nail entering the wood. It would seem strange to describe the impact of the hammer as a background condition to the nail's momentum". (Laland 2015)
In our argument, cultural transmission can represent the impact of the hammer and the selective gradient the nail's momentum. We hence consider cultural transmission as the causal factor triggering the selective gradient that ultimately leads to transmission mechanisms evolution.
If we accept the logic that cultural transmission is a relevant evolutionary factor for the spread of lactose absorption alleles, as today is widely accepted, we consequently should embrace the perspective that culture is a relevant evolutionary factor for the evolution of those transmission mechanisms that built up the long course of language and cumulative culture co-evolution. Bringing this argument to its theoretical consequences, we think that cultural transmission should be considered a relevant evolutionary factor shaping not only language current features (Tamariz and Kirby 2014), but, more strongly, the language-ready brain. In fact, language evolution can be depicted as an evolutionary history of recruiting (*exapting*) previously evolved mechanisms and capacities, a process capable of building up higher and higher-fidelity transmission mechanisms.
FOXP2 human variant fixation can be taken as a clear example of a component of the language-

ready brain, in which the role of culture should be considered not as a mere proximate cause, but rather as a relevant evolutionary factor. In fact, “It seems unlikely that *FOXP2* triggered the appearance of spoken language in a nonspeaking ancestor. It is more plausible that altered versions of this gene were able to spread through the populations in which they arose because the species was already using a communication system requiring high fidelity and high variety.” (Fisher and Ridley, 2013). This suggestion means that in a population already relying on a learned communication system, a genetic variant providing enhanced communication capacities would spread rapidly, as testified by the positive selection signals found on FOXP2 (Enard et al. 2002). The selective pressures for such a genetic variant would be stronger in a population already relying on learned communication. Human FOXP2 variant can be the product of a gene-culture co-evolutionary process, with cultural transmission as the evolutionary cause (and not just the background condition) that generates the selective pressures that spread the variant.

We find this logic quite consistent with the assimilate-stretch principle proposed by Dor and Jablonka (2000; 2014), according to which innovation arises through plastic phenotypic adjustment and in presence of consistent selective pressures advantageous variants are genetically assimilated in the population. These selective pressures are generated within the cultural niche characterized by social learning of a certain communication system (say, a protolanguage) and its cultural transmission. Hence we see cultural transmission playing a clear evolutionary causal role. As in the case of the spread of lactose absorption alleles, a genetic variant can be the consequence rather than the cause of behavioral adjustment, turning the traditional logic, according to which genes are always the prime movers, upside-down.

Attributing an evolutionary causal role to cultural transmission might have an interesting theoretical consequence:

1) a shift in the definition of what has to be considered an evolutionary process (Laland 2015). Typically, the SET approach confines the definition of an evolutionary process to those processes directly affecting gene frequencies across generations (mutation, selection, drift, flow). This approach however attributes an unjustified causal primacy to the genetic level. The EES approach instead proposes to widen the definition of evolutionary process to those processes that are capable of systematically bias selective pressures, even though not directly or immediately affecting gene frequencies, hence niche construction and developmental bias. In this perspective, genes are no longer the main characters of the evolutionary theater, but rather evolution is represented as a complex interplay of mechanisms, processes and causal factors displayed across the biological hierarchy. More importantly, this approach allows to inquire the nature of the selective pressures and genes are treated as the resulting outcome of the action of selective pressures and other

evolutionary processes.

We argue cultural transmission, intended as the causal trigger of phenomena such as lactose absorption alleles spread or selective gradients for high-fidelity transmission mechanisms, should be considered an evolutionary process. Even though it does not modifies gene frequencies directly, it can be considered a process that modifies the selective pressures which stand upstream from the selected gene frequencies.

Distinguishing between evolutionary causes and evolutionary processes is not trivial: they are separate but interrelated concepts. The question about causation is an epistemological question; the question about the process is a scientific-mechanistic question that allows to understand the details of a complex set of events. We argue that cultural transmission can be considered an evolutionary cause when it can trigger a selective event, and at the same time it can be considered an evolutionary process as it fits, in our view, the broadened definition proposed by the EES general conceptual framework.

2) causality between the three factors identified above (transmission mechanisms, selective gradient, cultural transmission) flows in a feedback circle, in what has been labeled *reciprocal causation* (Laland et al. 2015). If transmission mechanisms and the selective gradient can be identified as proximate mechanisms and ultimate causes respectively, cultural transmission is the gear playing a linking role, allowing feedback causal relationships between the previous two.

Therefore, we see the insufficiency of the proximate-ultimate distinction in catching the causal roles in play here (Laland et al. 2011). A different model of biological causality should be developed to cope with the limits of the proximate-ultimate distinction. Reciprocal causality is a first step in this direction (Laland et al. 2015) but we believe it can be integrated with further analyses, for example a multilevel perspective (Martinez and Esposito 2014), or a graph theory-based approach (Otsuka, 2015). This area of research is promising and needs further inquiry.

3) The consequence of such an argument is that cultural transmission should be considered as an evolutionary cause shaping not only language current features (Tamariz and Kirby 2014), but, more strongly, the language-ready brain. This stance follows from 2 points: a theoretical one and an empirical one. The theoretical one is the adoption of the EES-inclined conceptual framework that leads us to consider cultural transmission as an evolutionary cause and an evolutionary process, entangled in feedback relationships with other proximate mechanisms and ultimate causes; the empirical one is the current evidence coming from hominin evolution suggesting that cultural transmission has been in place at least since the origin of genus *Homo,* or even before, accompanying the building up of what today we call the language-ready brain. Hence, we believe it is inappropriate to consider the language-ready brain as a product of biological evolution alone. We

argue instead that explanatory pluralism (biological and cultural intended as distinct and related evolutionary processes) should be adopted in order to explain the language-ready brain evolution, referring to it as an overlapping of both biological and cultural evolutionary factors in what we labeled an integrative perspective (see fig. 1).

We argue this represents a crucial theoretical shift to understand the evolutionary factors in play in language evolution, and this is possible thanks to a EES-inclined theoretical framework.

5. Eco-evolutionary feedback loops: the Gradualism and Punctuationism debate

Evolutionary feedback loops can accelerate evolutionary change, making it compatible with an ecological time-scale rate of change (Post & Paklovacs, 2009). Gene-culture co-evolution is exactly the kind of process in which dynamics occurring at different time scales (cultural and biological change) can match. The evolutionary response can therefore result in an accelerated rate, producing a typical punctuated pattern, that is a burst of change preceded by relatively long period of stasis.

Moragn et al. *(*2015) selective gradient hypothesis relies exactly on a gene-culture co-evolutonary process, that is an eco-evolutionary feedback loop: in a population of individuals relying on learning and transmission mechanisms, the appearance of a genetic variant enhancing the efficiency of learning and transmission would have generated a significant advantage in the individuals possessing it, thanks to a frequency-dependent selection, hence it would have spread rapidly. The logic of this evolutionary mechanism is in principle compatible with what Dor & Jablonka argument (2000; 2014), the *assimlate-stretch principle,* in order to explain language evolution.

As a matter of fact, from the analysis of the archeological record, we can observe a rather punctuated pattern of spread of the lithic industries. Oldowan technology appeared approximately 2,5 mya and its stasis lasted approximately 700ky; Acheulean technology appears rather neatly around 1,7 mya and lasted quite unvaried until approximately 100kya. We can observe instead a burst of diversity in the archeological record in more recent years, starting from 300-200kya, suggesting that a certain threshold might have been overcome (d'Errico and Banks 2013).

However, even if we accept the argument that language have co-evolved with cumulative culture, this does not allows us to make inferences on whether cognition or communication systems followed the same apparently punctuated pattern showed by the evolution of material culture.

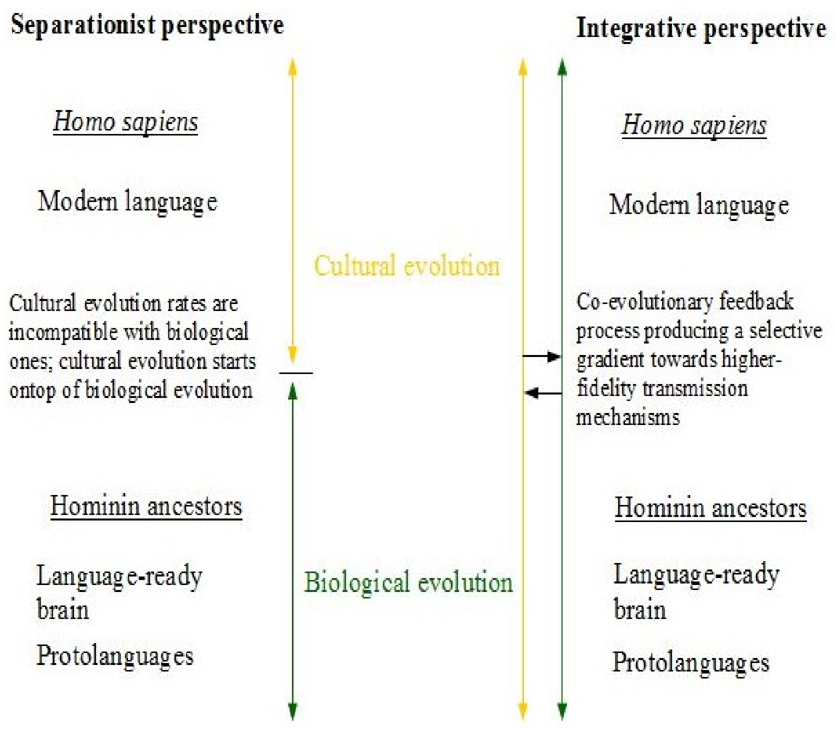

Figure 1. Separationist *perspective: the language-ready brain shaped by biological (genetic and epigenetic) evolution and modern language, as the product of cultural evolution; cultural transmission is associated only to the appearance of* Homo sapiens*; cultural evolution starts on top of biological evolution and their interaction is considered incompatible (Christiansen and Chater 2008).* Integrative *perspective: cultural evolutionary processes have acted along with biological evolutionary processes in a co-evolutionary feedback loop at least since the emergence of genus* Homo*; it follows that cultural transmission must be considered an evolutionary causal factor shaping the language-ready brain (Morgan* et al. *2015).*

Culture, communication and cognition are three strictly interrelated elements here, but their evolution could have in principle followed different rates. A punctuated pattern of cultural change is not in principle inconsistent with a more gradual accumulation of cognitive modifications that would have led to overcoming a certain threshold in communicative or cultural capacities. In fact, “the appearance of Acheulean tools may have additionally been contingent on the evolution of other aspects of cognition, such as technical comprehension or the hierarchical planning of actions, as well as demographic and socio-ecological factors. Accordingly, the extraordinary length of the Oldowan stasis could indicate that a large number of limiting factors needed to be overcome before innovations could appear and spread” (Morgan et al. 2015, p. 6)

Gradual accumulation of cognitive modifications and punctuated change of communicative capacities or cultural products are not inconsistent elements in a co-evolutionary dynamic based on threshold effects. Positive feedback processes typically scale up in rate after overcoming a certain threshold value. If a feedback dynamic is the actual process underlying the co-evolution of cumulative culture and (proto)language, and given the initial stasis of cultural evolution relying on low-fidelity transmission mechanisms, it is possible that it took a rather long amount of time to overcome some of the limiting factors (that other apes have never overcome) associated to the simplest forms of transmitted hominin culture. Cultural mitigation of selection might also have played a role in overcoming these limiting factors (Suman and Pievani 2015). Once these limitations, of various nature (cognitive, demographic, morphological, life-history, socio-ecological factors), where overcome, more complex forms of protolanguage and language might have appeared (what Pavlicev et al. 2016 label bio-cultural epicycles).

The eco-evolutionary feedback present in gene-culture co-evolutionary dynamics in principle makes the old antagonistic debate about gradual and punctuational rates of change in language evolution rather sterile, as different elements involved in language evolution (culture, communication, cognition) may have co-evolved, changing at different rates. The observed punctuated pattern of material culture evolution does not rule out the possibility of a gradual accumulation of biological (genetic, epigenetic, neural, cognitive) changes that at a certain point might have crossed a threshold value, scaling up the speed of observable change, consistently with co-evolutionary feedback processes. We retain more important to focus, rather than on the observed pattern (gradual or punctuational), also depending on the scale of observation, on the nature of the underlying process, that is the interaction between biological and cultural evolutionary processes: in this sense, we argued against a separationist perspective, depicting cultural evolution as a process that almost substitutes biological evolution, and in favor of an integrative perspective, in which biological and cultural evolution interact in a co-evolutionary feedback process in principle capable of producing bursts in evolutionary rates.

6. Conclusions

We did not explore here the underlying mechanisms that might have implemented the evolution of transmission mechanisms, but in such a co-evolutionary dynamics many specific cognitive mechanisms might have been co-opted to improve the effectiveness of information transmission: in principle, some traits today involved in the complex mosaic of the language faculty might have evolved as novel adaptations, not present in the ancestors (autapomorphies); other traits instead might have been already present as phylogenetic inheritance (synapomorphies), serving a different function not specifically related to linguistic communication, and could have been co-opted (exapted) for this novel functions (Fitch 2012; Suman and Pievani 2015).

We stressed here that the archeological and paleoanthropological data suggest that the interplay between cultural transmission, generation of new selective gradients and evolution of transmission mechanisms such as imitation, teaching and language has been in place for the long course of genus *Homo* evolution. This is why we argue in favor of what we labeled an integrative perspective and against a separationist perspective (Christiansen and Chater 2008; Arbib 2012; Pagel 2012) that simply juxtaposes cultural evolution on the top of biological evolution, the former almost substituting the latter. Acknowledging the role of cultural transmission in the process that led to the evolution of higher-fidelity transmission mechanisms, hence language, implies a significant theoretical shift, towards an EES framework of research, that may lead to interesting conceptual adjustments: widening the definition of evolutionary process; exposing the limits of the proximate-ultimate distinction, showing the need of a rethinking of biological causality in the direction of a reciprocal, as well as multilevel, view of causation; considering cultural transmission as a casual factor shaping the language-ready brain; a reconsideration of the debate on whether language evolved gradually or punctuationally, in light of considering language a multicomponent trait.

Today a proper model of feedback or reciprocal causation has only been suggested, but is not available yet to our knowledge; understanding why our species was able to separate its cognitive prowess from other species requires deepening our knowledge on the evolutionary feedback loop dynamics between biology and culture and developing a proper reciprocal or feedback model of causation may represent a crucial theoretical step in this direction.

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References

Antón SC, Potts R, Aiello LC (2014) Evolution of early *Homo*: an integrated biological perspective. Science 344:1236828.

Aoki K (1986) A stochastic model of gene-culture coevolution suggested by the "culture historical hypothesis" for the evolution of adult lactose absorption in humans. Proc Natl Acad Sci 104:10944–10949

Aoki K, Wakano JY, Feldman MW (2005) The emergence of social learning in a temporally changing environment: a theoretical model. Curr Anthropol 46, 2:334-340

Arbib M (2012) How the brain got language – the mirror system hypothesis. Oxford University Press, New York.

Berwick RC, Hauser MD, Tattersall I (2013) Neanderthal language? Just-so stories take center stage. Front Psychol 24:671 doi: 10.3389/fpsyg.2013.00671

Boeckx C, Benítez-Burraco A (2014) The shape of the human language-ready brain. Front Psychol 5:282

Boesch C (2003) Is culture a golden barrier between human and chimpanzee? Evol Anthropol 12:82-91

Bolhuis JJ, Tattersall I, Chomsky N, Berwick RC (2014) How could language have evolved? PLoS Biol 12, 8:e101934

Bolhuis, JJ, Tattersall I, Chomsky N, Berwick RC (2015) UG or not to be, that is the question. PLoS Biol 13, 2:e1002063

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. Chicago University Press, Chicago

Cavalli-Sforza LL, Feldman MW (1981) Cultural transmission and evolution. University of

Princeton Press, Princeton

Chater N, Christiansen MH (2010) Language acquisition meets language evolution. Cognitive Science 34:1131–1157

Chomsky N (2010) Some simple evo devo theses: how true might they be for language?. In: Larson RK, Déprez V, Yamakido H (eds) The evolution of human language: biolinguistic perspectives. Cambridge University Press, Cambridge

Christiansen MH, Chater N (2008) Language as shaped by the brain. Brain Behav Sci 31:489-558

Cosmides L (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. Cognition, 31:187–276

Curry A (2013) The milk revolution. Nature 500:20-22

d'Errico F, Banks WE (2013) Identifying mechanisms behind Middle Paleolithic and Middle Stone Age cultural trajectories. Curr Anthropol 54 (S8), Alternative pathways to complexity: evolutionary trajectories in the Middle Paleolithic and Middle Stone Age: S371-S387.

Danchin E, Charmantier A, Champagne FA, Mesoudi A, Pujol B, Blanchet S (2011) Beyond DNA: integrating inclusive inheritance in an extended theory of evolution, Nature Reviews Genetics 12: 475-486

Di Vincenzo F, Manzi G (2013) Social learning and the origin of the language faculty by means of natural selection. Journal of Anthropological Sciences 91:23-52

Dickins TE, Rahman Q (2012) The extended evolutionary synthesis and the role of soft inheritance in evolution. Proc R Soc B, 279:2913–2921

Dor D, Jablonka E (2000) From cultural selection to genetic selection: a framework for the evolution of language. Selection 1, 1-3:33-55

Dor D, Jablonka E (2014) Why we need to move from gene-culture co-evolution to culturally driven co-evolution. In: Dor D, Knight C, Lewis J (eds) The social origins of language, Oxford University Press, Oxford, pp. 15-30

Durham,WH (1991) Coevolution: genes, culture, and human diversity. Stanford Univ. Press, Stanford, CA

Enard W, Przeworski M, Fisher SE, Lai CSL, Wiebe V, Kitano T, Monaco AP, Pääbo S (2002) Molecular evolution of *FOXP2*, a gene involved in speech and language. Nature 418:869-872

Feldman MW, Laland KN (1996) Gene-culture co-evolutionary theory. Trends in Ecol & Evol 11, 11:453-457

Feldman, MW, Cavalli-Sforza LL (1989) On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In: Feldman MW (ed) Mathematical evolutionary theory. Princeton Univ Press, Princeton, NJ

Fisher SE, Ridley M (2013) Culture, genes, and the human revolution. Science 340:929-930

Fitch WT (2005) The evolution of language: a comparative review. Biol & Philos 20:193-230

Fitch WT (2008) Glossogeny and phylogeny: cultural evolution meets genetic evolution. Trends in Genetics 24, 8:373-374

Fitch WT (2012) Evolutionary Developmental Biology and Human Language Evolution: Constraints on Adaptation. Evolutionary Biology 39:613-637

Fogarty P, Strimling P, Laland KN *(*2011) The evolution of teaching. Evolution 65, 10:2760-2770

Gerbault P, Liebert A, Itan Y, Powell A, Currat M, Burger J, Swallow DM, Thomas MG (2011) Evolution of lactase persistence: an example of human niche construction. Philos Trans R Soc B 366:863– 877

Harmand et al. (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521:310-314

Hillert DG (2015) On the evolving biology of language. Front Psychol 6, 1796:doi: 10.3389/fpsyg.2015.01796

Holden C, Mace R (1997) Phylogenetic analysis of the evolution of lactose digestion in adults. Hum Biol 69:605–628

Jablonka E, Ginsbur S, Dor D (2012) The co-evolution of language and emotions. Phil Trans R Soc B 367:2152–2159

Kirby S, Hurford J (2002) The emergence of linguistic structure: an overview of the iterated learning model. In Cangelosi A and Parisi D (eds) Simulating the evolution of language. Springer

Kirby S, Cornish H, Smith K, (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language, Proc Natl Acad Sci 105, 31:10681-10686.

Kuhn T (1962) The structure of scientific revolutions. University of Chicago Press, Chicago

Lakatos I (1978) The Methodology of Scientific Research Programmes. Philosophical Papers, vol. 1, Cambridge University Press, Cambridge (UK)

Laland KN, Odling-Smee J, Myles S (2010) How culture shaped the human genome: bringing genetics and the human sciences together. Nature Rev. Gen. 11:137-148

Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T (2011) Cause and effects in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science 334:1512-1517

Laland KN, Odling-Smee J, Hoppitt W, Uller T (2013) More on how and why: cause and effects in biology revisited. Biol Philos, 28:719–745

Laland KN, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J, (2014) Does evolutionary theory need a rethink? Yes, urgently. Nature 514:161–164

Laland KN, Uller T, Feldman MW, Sterelny K, Mu¨ller GB, Moczek A, Jablonka E, Odling-Smee J. (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282:20151019.

Laland KN (2015) On evolutionary causes and evolutionary processes. Behavioral Processes 117-97-104

Laland KN (2016, in press) Culturing our mind. Princeton University Press, Princeton

Lepre CJ et al. (2011) An earlier origin for the Acheulian. Nature 477:82–85

Lewis HM, Laland KN (2012) Transmission fideliy is the key to the build-up of cumulative culture. Phil Trans R Soc B 367:2171–2180

Lieberman P (2015) Language did not spring forth 100,000 years ago. PLoS Biol 13, 2:e1002064

Martinez M, Esposito M (2014) Multilevel causation and the Extended Synthesis. Biol Theory 9:209-220

Mayr E (1961) Cause and effect in biology. Science 134:1501–1506

Mesoudi A (2011) *Cultural evolution – how Darwinian theory can explain human culture and synthesize the human science*. University of Chicago Press, Chicago and London

Mesoudi A, Blanchet S, Charmantier A, Danchin E, Fogarty L, Jablonka E, Laland KN, Morgan TJH, Mu¨ ller GB, Odling-Smee J, Pujol B, (2013) Is Non-genetic Inheritance Just a Proximate Mechanism? A Corroboration of the Extended Evolutionary Synthesis. Biol Theory, DOI 10.1007/s13752-013-0091-5

Morgan TJH, Uomini NT., Rendell LE, *et al.* (2015) Experimental evidence for the co-evolution of hominin tool-making and language, Nature Communications 6, 6029:1-8.

Odling Smee FJ, Laland KN, Feldman MW (2003) Niche construction – the neglected process in evolution. Princeton University Press, Princeton and Oxford

Odling Smee J, Erwin DH, Palkovacs EP, Feldman MW, Laland KN (2013) Niche construction theory a practical guide for ecologists. The Quarterly Review of Biology 84, 1:3-27

Otsuka J (2015) Using causal models to integrate proximate and ultimate causation. Biol Phil 30:19-37

Pagel M (2012) Wired for culture – the natural history of human cooperation. WW Norton & Company, USA

Parravicini A, Pievani T, (2016, in press) Multi-level human evolution: ecological patterns in hominin phylogeny. Journal of Anthropological Sciences, 94:1-16 doi 10.4436/jass.94026

Pavlicev M, Prum RO, Tomlinson G, Wagner GP (2016) Systems emergence: the origin of individuals in biological and biocultural evolution. In: Eldredge N, Pievani T, Serrelli E, Temkin I (eds) Evolutionary theory: a hierarchical perspective. The University of Chicago Press, Chicago, pp. 203-223

Pievani T (2011) An evolviong research programme: the structure of evolutionary theory from a lakatosian perspective. In: Fasolo A (ed) The Theory of Evolution and Its Impact. Springer-Verlag, Berlin, 211-228

Pievani T (2015) How to rethink evolutionary theory: a plurality of evolutionary patterns. Evolutionary Biology, DOI 10.1007/s11692-015-9338-3

Pievani T (2016), Evolved and abandoned: is Evolutionary Psychology really “evolutionary”?, in G. Andrade, ed. by, Defending Scientism, Editorial Laetoli, in press.

Post DM, Palkovacs EP (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Phil Trans R Soc B 364:1629–1640

Scott Phillips T (2007) The Social Evolution of Language, and the Language of Social Evolution. Evolutionary Psychology 5, 4:740-753

Scott Phillips TC, Kirby S (2010) Language evolution in the laboratory, Trends in Cognitive Sciences 14:411-417

Scott Phillips TC, Dickins TE, West SA (2011) Evolutionary theory and the proximate-ultimate distinction in the human behavioral sciences, Perspectives on Psychological Science 6, 1:38–47

Scott Phillips TC, Laland KN, Shuker DM, Dickins TE, West SA (2013) The niche construction perspective: a critical appraisal, Evolution 68, 5:1231–1243

Semaw S, Renne P, Harris JWK, Feibel CS (1997) 2.5-Million-year-old stone tools from Gona, Ethiopia. Nature 385:333–336

Simoons, FJ (1970) Primary adult lactose intolerance and the milking habit: a problem in biologic and cultural interrelations. Digest. Dis. Sci. 15:695– 710

Sterelny K (2012) Language, gesture, skill: the co-evolutionary foundation of language. Phil Trans R Soc B 367:2141–2151

Stout D (2011) Stone toolmaking and the evolution of human culture and cognition. Phil Trans R Soc B 366:1050–1059

Suman and Pievani (2015) The evolution of human language: an alternative scenario. Paradigmi Rivista di Critica Filosofica 2:173-196

Suman F (2016, in press) An updated evolutionary research programme for the evolution of language. Topoi

Tallerman M, Gibson KR (2012) Introduction: the evolution of language. In: Tallerman M, Gibson KR (eds) The Oxford Handbook of language evolution, p. 1-35, New York

Tamariz M, Kirby S (2014) The cultural evolution of language. Curr Op Psychol 8:37-43

Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Phil. Trans. R. Soc. B (2009) 364, 2405–2415

Tinbergen N (1963) On aims and methods in ethology. Zeitschrift fu¨r Tierpsychologie 20:410–433

Tooby J, Cosmides L (1992) The psychological foundations of culture. In: Barkow J, Cosmides L, Tooby J (eds) The adapted mind: evolutionary psychology and the generation of culture. Oxford University Press, Oxford, pp 137–159

Watt WB (2013) Causal mechanisms of evolution and the capacity for niche construction. Biol Phil 28:757–766

West-Eberhard MJ (2003) Developmental Plasticity and evolution. Oxford University Press, Oxford

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Culture in chimpanzees. Nature 399:682-685

Whiten A, Hinde RA, Laland KN, Stringer CB (2011) Culture evolves. Phil Trans R Soc B 366:938–948

CONCLUSION

1. Teaching and language

Another point we would like to touch briefly here in the conclusions is the relationship between the evolution of teaching and the evolution of language discussed in Laland (2016, in press). Teaching can be defined as the behavior that enhances the fidelity of the information transmission between tutor and pupil, hence, an active facilitation of learning in others. Understanding teaching is then fundamental for our purpose, as language is seen as a particular form of teaching, that is verbal teaching. Under this perspective language is part of a more broad view that is the evolution of teaching. And teaching evolution itself in turn is part of a broader frame which is the evolution of cooperation. That's why this should be intended as one long argument for the evolution of language, as we discussed in the Introduction of this work.

In Morgan *et al.,* (2015) language was treated experimentally exactly as a form of (verbal) teaching. Teaching has an unusual phylogenetic distribution (Fogarty et al., 2011): it is found in cheetahs, domestic cats, meerkats (feeding behaviors, like eating scoprions), ants (tandem running), a bird named pied babbler, tamarin monkeys and bees. Mechanistically speaking, these cases are very different from one another. No compelling evidence for teaching instead has been found in dolphins, apes and elephants, which are usually accounted as brainy animals.

Teaching is linked to the evolution of social learning, learned communication and cooperation. Despite the fact it can be considered a form of cooperation, teaching is not usually formally explained with theories of evolution of cooperation. Cooperation usually works with a donor giving matter (food, for instance) to a receiver, but it also works with the exchange of useful or adaptive information: in the case of teaching in fact we can talk of fitness-enhancing information provided by the tutor to the pupil.

Mathematical modeling for the evolution of teaching were developed by Fogarty et al. (2011). Teaching occurs at a cost, that is the cost that the tutor pays to school the pupil and providing him with fitness-enhancing information. This is supposed to be the reason why teaching is more likely to evolve through kin selection eventually resulting in a positive increase of inclusive fitness.

Animals like chimpanzees, very good in both asocial (trial and error) and social (copy) learning, would not invest in teaching, which is costly, as long as they can solve all their tasks relying on less costly strategies. It follows that the taught skill will not be easy to acquire, but rather it is expected to be quite sophisticated, as the cost should be translated in a significant advantage (resulting in fitness increase).

Although language today is usually intended as an almost cost-free communication system (each utterance involves a minimum cost in terms of energetic investment), language evolution might have involved several costs, both at the individual level and at the social level. At the individual level, lowering the larynx represented a rather high cost as it raised the risk of choking (Fitch and Reby, 2001); such a risky adaptation could only have been reached through a significant benefit, which could be the one provided by language acquisition. At the social level, a reorganization of the social group was a necessary condition to increase social tolerance among individuals and allow more information exchange through cultural transmission: we explored the plausibility of the self-domestication hypothesis in the first chapter and we analyzed the causal role of cultural transmission in the evolutionary process that led to the emergence of language in the third chapter. In such a closer social condition, teaching might have spread more easily.

However, instead of building wrong expectations on teaching, believing to find it necessarily among "smart" animals, which can still solve their tasks relying on trial and error and social learning, teaching should be expected in those contexts in which the exchange between pupil and tutor is frequent, so mainly among kin. As the social structure has changed during human evolution, it is plausible that in a first stage exchanges among kin might have represented the context in which vocal experimentations were performed.

Of course, human teaching today is extended also among non-kin, and the same is true for language intended as exchange of information among non-kin. Moreover, language is today exploited to teach and transmit all sort of things, not necessarily related to higher fitness. However, this should not be seen as an obstacle to the kin selection hypothesis for the early stages of language evolution (Fitch, 2004, 2007; Falk, 2009; Laland, 2016). The current use of a trait is not informative of its evolutionary path (Gould and Lewontin, 1978), as language, once in place, has almost certainly been exapted for the most variable tasks. More specifically, language, might have co-evolved with the complexification of cumulative culture and the cognitive traits exploited to support it, in an evolutionary feedback process of reciprocal causation.

Dean et al. (2012) inquired which kind of cognitive traits might have been related to the evolution of teaching, language and cumulative culture, in an experiment involving human kids, chimpanzees and capuchin monkeys. The experiment consisted in the solution of a puzzlebox with three levels of increasing complexity, and three corresponding levels of increasing reward. As expected, children performed better, showing capacity for teaching each other with task-relevant communication and gesture. This result can be also considered an indirect support for the cultural intelligence hypothesis, according to which humans possess "a species-specific set of social-cognitive skills, emerging early in ontogeny, for participating and exchanging knowledge in cultural groups"

(Herman et al. 2007; see also Van Shaik and Burkart, 2011, Van Shaik et al., 2012).

Moreover, relying on teaching, that is transmission at a cost of not-so-easy-to-acquire behaviors or other cultural traits, might have been advantageous once cumulative culture grew in complexity and diversity. In fact, Fogarty et al. (2011) also tested this scenario with their mathematical models, obtaining the expected results that teaching is more advantageous in the presence of cumulative culture, namely teaching is more probable to spread, it is more profitable. This is a confirmation that teaching is likely to be exploited when the transmitted trait is not easy to acquire through trial and error or copying strategies.

Another relevant point for our discussion here is that species relying on teaching are also good cooperative breeders. We discussed in chapter 1 some aspects through which cooperative breeding might have emerged in genus *Homo* evolution, focusing in particular on how prolonged juvenile dependency might have contributed to the spread of teaching and vocal experimentation (Fitch, 2004, 2007), hence providing another fundamental brick for the ground on which language could blossom.

Summing up, it can be noticed that a cluster of relevant factors must be clarified in order to understand the onset of language evolutionary trajectory.

Once again we want to stress how inadequate are mono-functional, atomistic, unidirectional and externalist explanations, whose profile we have outlined, in the Introduction, referring to them as to naïve evolutionism; we brought the example of the Social Brain hypothesis (Dunbar and Shultz, 2007) highlighting a general tendency associated to the SET viewpoint of considering one single variant (for example group size) as causally relevant and predicting for a complex trait like brain size.

Instead, Laland and colleagues' work (Laland, 2016) revealed how multiple variants (quantitative measures of rates of innovation, social learning, tool use, extractive foraging, tactical deception, diet breadth, fruit in the diet and group size; see Reader and Laland, 2011) are interrelated in the prediction of a particular complex measure (such as intelligence) and how these components have co-evolved, causally influencing each other reciprocally. In this sense, it is inappropriate to search for a *prime mover* both for the evolution of human intelligence and for the evolution of human language: we argued in the Introduction that the inclination to look for a prime mover that characterizes the SET theoretical framework is associated to a causal primacy attributed to genetic inheritance. In fact, for the evolution of language many speculative hypotheses have been proposed: cooperative hunting, costly ornament allowing females to assess male quality, substitute for grooming, pair bonding, mother-child communication, gossip, tool making, tool for thought (see Szamado and Szathmary, 2006 for a review). We argued that they represent monofunctional explanations, or just so stories, identifying one single cognitive or behavioral trait responsible for the evolution of the whole language faculty.

We believe that the work brought forward by Kevin Laland and colleagues in the last years and quickly summarized at the end of the Introduction and here in its crucial points (see Laland, 2016 for a more appropriate synthesis) represents a fruitful conceptual framework shift, along some pivotal theoretical assumptions that overcome the SET logic and that characterize the EES proposal. In this sense, chapter two shows how the key epistemic elements of the EES can be exploited for a more accurate account: niche construction, inclusive inheritance, phenotypic plasticity, developmental bias, reciprcal causation, constructive development and an explanatory pluralism against the prime mover logic.

We believe that this explanatory structure makes more justice to Ernst Mayr's suggestion that biology is the science of multiple causes (Mayr, 2005). We tried to adopt this very viewpoint also in the published papers constituting all the chapters of this work and in particular we dedicated chapter two to show why the adoption of this theoretical framework might result crucial for the studies to come. In the evolutionary explanation, multiple underlying causes are responsible for the emergence of a certain trait and this becomes apparent when language, defined as a mosaic of traits, is taken into account; in chapter 3 we argued that a reciprocal causation model is required, even though such a causal model still has to be developed in literature to our knowledge.

Recapping the argument presented in this work, we try to keep together some aspects of human evolution in order to clarify the emergence of language.

Humans alone possess cumulative culture because humans alone possess sufficiently high fidelity information transmission mechanisms, including an unusually accurate capacity for imitation, teaching and language.

Theoretical findings suggest that natural selection might have favored more efficient means of cultural transmission and higher-fidelity social learning. But why humans alone? High-fidelity transmission is required for cumulative culture, but then how our ancestors achieved it? Here in the conclusions, we are suggesting, with Laland's argument, that teaching might have played a crucial role. Stringent conditions (low costs, accurate and effective, strong relatedness) should be met for teaching to evolve, as it is rare in nature; cumulative culture itself relaxes the conditions that restrain teaching to evolve and a self-domestication condition, which we explored in chapter one, might have favored the spread of such a trait once it was already present in smaller groups. In fact, our ancestors 2mya were structured in small kin-structured groups and teaching is more efficient and likely to evolve among kin. Also, cooperative breeding (allomothering and alloparenting), long period of juvenile dependence (extended childhood), a change of diet (determined by the use of fire) are among the factors that we considered in chapter one that might have favored this change in the ecological conditions. From this perspective niche construction and more precisely counteractive niche construction or cultural mitigation of selection are among the fundamental processes that influenced human evolution.

The co-evolution of teaching and cumulative culture in a self-domesticated condition increased transmission effectiveness and lowered the costs of the transmission of complex behavior whose adaptiveness was positively selected: language could have followed this evolutionary logic.

Let's state this argument once again: language is a form of high-fidelity transmission; high-fidelity transmission is required for cumulative culture; cumulative culture generates the (cultural) selective environment to make teaching highly adaptive; language is a high-fidelity form of teaching. Language could have co-evolved with cumulative culture as a high-fidelity form of teaching, allowing the transmission of complex behaviors and cultural traits.

Is there some form of circularity in this explanation? No, because this represents a co-evolutionary logic and a form of feedback causality. But in order to appreciate this logic, we argued, in chapter three, that a theoretical shift in our understanding of evolutionary causality is required, moving away from a conception of unidirectional causation typical of the SET view and moving towards a conception of feedback causality (see fig. 6) typical of the EES framework.

“It sounds paradoxical that teaching should both explain the advent of human cultural complexity and be the product of it, but that is exactly what we should expect if a feedback mechanism, like Wilson's cultural drive, is operating. In fact, evolutionary feedback mechanisms help to explain a lot more about the human condition than I have touched on so far, including that quintessentially human attribute, our language” (Laland, 2016, p. 161)

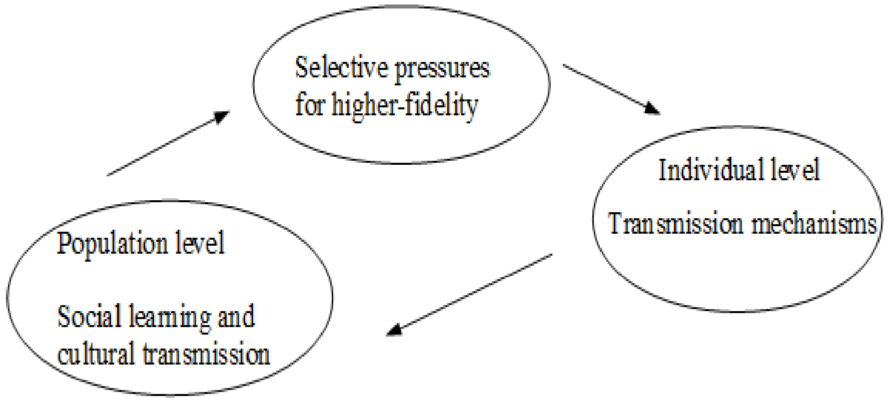

Figure 6.
Cultural transmission itself is nourished by individual level ontogenetic mechanisms (imitation, teaching, language), generating selective pressures for higher-fidelity in a population relying on such mechanisms. A feedforward process is in play and causality is reciprocal.,

2. The Cultural Assimilation model: a tentative sketch

Referring to cultural evolutionary dynamics, Lewis and Laland (2012) identify three main cultural processes through which information is retained or lost: novel invention (generation of new traits), modification (refinement of existing traits) and combination (bringing together two established traits to generate a new trait). The study develops a simple cultural transmission model and, beyond finding that transmission fidelity is the key ingredient for cumulative culture, it finds that progress in cumulative culture is dependent more on trait combination than on trait invention or modification. However, "novel invention, modification and combination are all forms of innovation" (Lewis and Laland, 2012, pp. 2172-2173).

Creative individuals are usually considered the source of innovations in cultural evolution studies. However, Dor and Jablonka (2014) suggest that language, intended as a cultural collective entity that exists above and outside the individual (meaning that individuals come in a world in which language is already outhere spoken by the community in which they are born), is subject to phenomena of *collective innovation* (see also Dor, 2015; Muthukrishna and Henrich, 2016). As a cultural collective entity, a language is built by a plurality of individuals across generations and it represents a much larger phenomenon than whatever could be detected at the level of the individual or looking only inside the brain. Communication, by definition, exceeds the single individuality and involves at least a sender and a receiver, up to a community of speakers. In language change dynamics, it is apparent that linguistic innovations "emerge and make their way towards stabilization and acceptance through implicit social negotiation" (Dor and Jablonka, 2014, p. 24). James Hurford (2014) makes an illuminating simple example regarding these dynamics: we cannot say who invented the way of saying "I was like [pause] Wow!", it could be one individual or several individuals, a sort of monogenesis or polygenesis; but this "innovation" spreads and is accepted by the members of the community of speakers as a social innovation, collectively invented and immediately put at use. Does this modality of innovation exist in other animals or is this social innovation a uniquely human dynamic?

We saw that cumulative culture can be considered one of the hallmark of humans compared to other non-human primates, but Dor and Jablonka (2014) make a step further proposing that "the suggestion that the major capacity that separates us from the apes is the social capacity of collective invention" (Dor and Jablonka, 2014, p. 17). Primate species are capable of exhibiting complex cultural traits (Whiten *et al.*, 1999), but as for cultural dynamics of innovation primates would be incapable of generating innovation as a community.

Although creativity and innovation are usually associated to the *lone genius*, humans, thanks to the evolution of their high level of cooperativeness (for which the self-domestication hypothesis is a tentative even though plausible explanation that we explored in the first chapter), are capable of something that Dor and Jablonka define *group genius*, that is a joint action in which individuals cooperate in intensive, motivated and trustful communication, giving rise to new linguistic, behavioral, communicative or generally cultural inventions. Social play in human children could be taken as a good case-study to model such dynamics and comparative behavioral experiments performed among children and chimpanzees seem to confirm the hypothesis that human cognition has an evolved inclination towards social inputs and cooperation (Hare *et al.*, 2007; Dean *et al.*, 2012).

But does collective innovation play a role only in language change (that is how natural languages evolve in the glossogenetic timescale) or rather it might have played a role also in language origin and evolution? Dor and Jablonka answer in a co-evolutionary sense arguing that language facilitates social interactions and they suggest that language may have co-evolved with human capacity for collective collaborative creativity.

It has to be said, however, that collective innovation is not defined in details in Dor and Jablonka's work and it remains a little too vague concept, although with extraordinary heuristic potential. Future work should refine better the definition of collective or social innovation in comparison to animal cultural capacity to innovate. In fact, two pivotal elements are key in cumulative culture: 1) transmission fidliety (Lewis and Laland, 2012) and 2) innovation capacities; non-human primates are capable of innovation capacities although limited (Charbonneau, 2015), collective innovation might be a specific feature that distinguish humans from other non-human primates.

Along this lines of research, recent studies proposed that the unparallelled capacities for innovation in our species are to be intended as emergent properties (Muthukrishna and Henrich, 2016; Griffin, 2016) of our cultural learning abilities, applied within our culturally complex societies and social networks, stressing that rates of innovation are heavily influenced by sociality, transmission fidelity and cultural variance, with these factors at the same time shaping each other (Muthukrishna and Henrich, 2016). Regarding languages, they also argue that transmission efficiency is affected by sociality and languages with more speakers are more efficient (Lupyan and Dale, 2010; Bromham *et al.*, 2015). Muthukrishna and Henrich (2016) in particular argue that our societies and social networks act as collective brains, with individual members acting like neurons in a neural network, each one of them possessing an individual brain evolved for, and entirely dependent on, the acquisition of culture and language: therefore, our cultural brains (see the cultural intelligence hypothesis by Herrmann *et al.,* 2007) evolved in tandem with our collective brains.

The collective brain metaphor might present some serious theoretical difficulties; for example a cell like a neuron, possesses all the genetic information of the organism in which it is located, while an individual in a society does not retain all the cultural information within that very society. However, this metaphor allows to frame collective innovation as an emergent property, leading to some useful empirical consequences. Griffin (2016) reviews the last decades studies on animal innovation (Reader and Laland, 2003) and proposes a fundamental paradigm shift: innovation has long been treated as single behavioral trait, a single product of cognition and a direct target of selection. Griffin argues that recent evidence suggests that innovativeness should be intended as an emergent property of a larger array of underlying traits evolved to cope with environmental variation. This also suggests that innovation could not be a direct target of selection, but rather a by-product of selection occurring on underlying traits. This might be in principle consistent with the study conducted by Laland and colleagues (Reader and Laland, 2002; Reader *et al.*, 2011) on the evolution of primate general intelligence. If we consider the capacity of innovation and more specifically the capacity for collective innovation a fundamental component for the evolution of cumulative culture, once again a co-evolutionary model seems to result the most accurate one to account for the complex interrelations between various traits and components influencing and shaping each other reciprocally.

Going back to Dor and Jablonka (2014) viewpoint, we also believe that their proposal on the evolution of language shows a theoretical continuity with the cultural drive hypothesis, extending some of its arguments to the evolution of language.

Allan Wilson's cultural drive hypothesis original idea (that we presented in the introduction of this work) was based on the hypothesis that an advantageous habit (innovation) emerges, it spreads through social learning, selection fixes it, and the selection regime is influenced by innovations themselves. Innovation, as we already said, is usually associated to individuals, but Dor and Jablonka argue that humans are characterized by social, collective capacity for innovation, hence coming from the cultural level. Moreover, Dor and Jablonka proposal follows a cultural-phenotype-first logic and a gene-as-folowers logic: a novel trait emerges as a plastic behavioral adjustment to environmental conditions and, given a certain stability in selective pressures, the trait gets fixed in the population. The first way a trait can get fixed in the population is the *genetic assimilation* model, proposed in the assimilate-stretch principle by Dor and Jablonka (2000) for the evolution of language (that we explored in the Introduction of this work): a novel trait, emerged through cultural innovation, given the consistency of selective pressures, can be genetically fixed in the population once it emerges as genetically expressed (see also the Baldwin effect); this model was originally proposed for language evolution but, in principle, might be extended for the evolution of cumulative culture. However we would like to add that there is another way, in our opinion, through which the trait can get fixed in the population.

We would like to characterize the second way through which a cultural innovation can get fixed within the population without involving genetic fixation but only involving the cultural level, hence labeling it the *cultural assimilation* model: when a novel trait emerges, both through individual or collective innovation, instead of being fixed at the genetic level, we argue it can get fixed at the cultural level. This is possible if we take seriously the theoretical consequences of embracing an inclusive inheritance framework: culture, intended as a system of inheritance, is a repository of information, capable of storage, replication and modification processes. Intended as a system of information transmission, the cultural level contributes to phenotypic expression in the organism. In fact, according to the inclusive inheritance perspective, multiple inheritance systems contribute to phenotypic variation across generations and according to a constructive view of development, genetic expression is an open-ended process and the organismal phenotype is the result of the interaction of genetically modulated information and environmentally (hence also cultural) modulated information.

Culture can work as a collective repository of information that is shared by a multiplicity of individuals: this corresponds to the concept of *cultural archive* in Pavlicev *et al.,* 2016. This information can be adaptive and maintaining this information across generation can result crucial for the survival of a population. A novel behavior can emerge, it can result adaptive and it can spread among individuals through cultural transmission, and an efficient communication system might help spreading this adaptive behavior or cultural trait. The recipe to perform effectively this adaptive behavior can get fixed in the communication system and as such it can spread with teaching to other individuals. So without involving a costly genetic fixation, but only adjusting the available endowment and exploiting the degrees of plasticity of the organism, a certain behavior can get fixed culturally in the communication system in the form of adaptive information that allows to perform effectively an efficient behavior. Language would be the communication system that allows such a cultural assimilation better than any other culturally emerged system, due both to its high-fidelity transmission features and to its degrees of freedom in integrating in principle an infinite number of novelties starting from a finite set of elements and combinatory rules (discrete infinity: making infinite use of finite means).

In such a model, plastic adjustment capacities of the individuals (and the population) are a fundamental ingredient, and plasticity is expected to be favored by selection in such conditions. As a matter of fact, in the course of human evolution, populations had to cope with different changing environment and construct their niche in order to recreate adaptive conditions and plasticity might have been significantly favored; moreover, as behaviors grew complex and complex, a communication system capable of storing and reproducing adaptive information might have been positively selected. We explored the hypothesis according to which a selective gradient from lower to higher-fidelity transmission mechanisms co-evolved with the evolution of cumulative culture in human evolution in chapter two and three, and Morgan *et al.*, 2015 experiment is a first tentative attempt to provide experimental support to this hypothesis.

Moreover, such a *cultural assimilation* model, here just sketched, makes some predictions: it predicts that a certain amount of adaptive information in humans is stored not at the genetic level, but rather at the cultural level. Access to this information occurs through various forms of mimesis (observation, emulation, imitation), teaching (simple, gestural, verbal) and other forms cultural transmission; this is a much more rapid and effective way to get access to adaptive information than the expression of developmental programs extracting information for adaptive traits from genes. As a matter of fact, human diversity today is scant at the genetic level and extremely rich at the cultural level.

This proposal of a *cultural assimilation* model is derived from taking inclusive inheritance to its natural consequences: genetic inheritance is not the exclusive way through which information can be transmitted from one generation to another; cultural transmission can be another much more rapid source of adaptation for organisms relying on culture as a plastic evolutionary strategy.

Summarizing, we are essentially proposing a partial integration (or expansion) to the asimilate-stretch principle model (Dor and Jablonka, 2000) which initially stressed genetic assimilation. Today we know that language is best described as a mosaic of traits (Hurford, 2003; Fitch, 2012) that have been exapted from already existing traits such as pre-synactic, pre-semantic and pre-symbolic features that were probably present long before the appearance of *Homo sapiens* in other hominins. Some of these traits are older and some more recent, made of both “innate” or more genetically modulated components and “acquired” or culturally learned elements. The assimilate-stretch principle (see fig. 5 in the Introduction) provides an abstract model of the evolutionary process that might stand at the basis of the interaction between typical biological (genetic) evolution and cultural evolutionary dynamics influencing the former. Despite the fact this model was originally proposed for language evolution, it can be easily extended to any cultural capacity, broadly intended; in other words, it can be a valid model also for the evolution of cumulative culture. As a matter of fact it is much more likely that genetic assimilation occurred for older and fundamental traits, such as mnemonic capacities or information processing capacities (already exploited in other tasks), rather than for more recent specifically linguistic features such as syntactical rules. Moreover today hypotheses for cultural acquisition of syntactical rules, not involving specific genetic or cognitive requirements, are in principle available, such as the Iterated

Learning Model (see Kirby and Hurford, 2002).

Intending culture as a collective repository of information (*cultural archive*, Pavlicev *et al.*, 2016) we propose that cultural assimilation might occur in parallel to genetic assimilation: the result would be a complex system in which certain parts are more genetically modulated than others that will remain "culturally modulated", that is learned through cultural/behavioral transmission. The complex system will rely both on genetic and cultural systems of inheritance, in agreement with an inclusive inheritance perspective.

This proposal is only at a tentative stadium here, as it should be better defined under which specific conditions it is advantageous to genetically assimilate a trait and under which conditions it is advantageous to culturally assimilate a trait. However, we believe this abstract model might have some merit in describing the co-evolutionary process (integrating biological and cultural evolution) at the bases of the origin and the evolution of language and more boradly it can be extended in principle to the evolution of cumulative culture. Future work on these issues is however required.

3. Language as a bio-cultural major transition

In light of what we discussed so far, we believe that characterized as an information storage and replication system, it is legitimate to intend language as a *major transition* in evolution (Maynard Smith, Szathmary, 1995; Jablonka, Lamb, 2006).

In fact, a major transition in evolution is defined as a change in the way information is stored, transmitted or interpreted in evolution. So for example, despite being a fundamental turning point in evolutionary history, the transition from water to land is not intended as a major transition sticking with the definition just provided, because it doesn't involve a modification in the way information is transmitted. Here we won't explore all the issues related to the concept of information in biology (see Stotz and Griffiths, 2011). Maynard Smith and Szathmary identify 8 major transitions in evolution:

(1) from replicating molecules to populations of molecules in compartments (protocells); (2) from independent genes to chromosomes; (3) from RNA as both an information carrier and enzyme to DNA as the carrier of information and proteins as the enzymes; (4) from prokaryotes to eukaryotes; (5) from asexual clones to sexual populations; (6) from single-cell eukaryotes to multicellular organisms with differentiated cells; (7) from solitary individuals to colonies with non-reproductive castes; (8) from primate societies to human societies with language.

Maynard Smith and Szathmary's work set the agenda for the biological studies of the 21st century;

however, we argue that, as it is strongly focused on the primacy of genetic information, it represents probably a typical SET approach. As we saw, the EES framework expands the concept of hereditary transmission of information beyond genetic inheritance, to epigenetic, environmental and cultural inheritance (Danchin *et al.*, 2011). We believe that Jablonka and Lamb proposal and Pavlicev *et al.* account go exactly in this direction especially regarding cultural inheritance, whose causal relevance in human evolution was treated in chapter three.

One of the fundamental logic through which these transitions occur consists of the formation of higher-level entities, with selection shifting from lower-level units to higher-level units, allowing them to benefit more by cooperating than by competing; in these processes a multilevel selection analysis shows how selection, at a certain point and under certain conditions, favors higher-level units (see Okasha, 2006 for an analysis of multilevel selection in the major transitions).

However not all the major transitions occur through the exclusive process of the emergence of a higher-level entity. For example, the transition from RNA to DNA follows a *division of labour* logic. The same is true for the 8th transition, that is the emergence of human cultural and linguistic societies: reliance on cultural transmission beyond genetic transmission plays a crucial role in this last major transition, the differentiation is more horizontal (*division of labour*) than vertical (higher-level entity emergence). As a matter of fact, when we refer to culture, we cannot talk of a higher level entity in the same way as we intend the transition from unicellular to multicelluar organisms; it would be a strong claim assessing that culture is itself an individual, or better a collective entity capable of self-reproduction. However, something analogous has been proposed by researchers like Terrence Deacon (1997) referring to language as a self-reproductive system adapting to human mind.

Pavlicev *et al.* (2016) also discuss culture within the major transition framework and they "hypothesize that any major transition in the evolution of life is accomplished through the origin of novel *kinds* of individuals". One of the new kind of individuals discussed by Pavlicev *et al.*, (2016) is what they call systems of human cultural coalescence or *epicycles* in human biocultural evolutionary dynamics.

"Cultural epicycles help to explain the pace of cultural innovation across late hominin evolution, its sporadic burgeoning for several hundred thousand years, and its explosive acceleration, especially among sapient humans, across the last hundred millennia or so" (p. 212). We explored the issue of evolutionary pace in biolcultural dynamics of eco-evolutionary feedback in chapter three, discussing also the debate on evolutionary patterns like gradualism and punctuationism (Suman, submitted).

We cannot explore here the theoretical, philosophical and conceptual consequences of claiming that culture is an individual at this point here (is it capable of self-reproduction? Is it a level in the biological hierarchy?) despite this crucial topic would deserves more inquiry in the future (for a tentative definition of culture and its differentiation from cumulative culture, see Dean et al. 2013 and Noël Haidle et al. 2015)

In Pavlicev *et al.* view, culture (broadly defined as learned information), traditions (group level fixed behaviors) and single cultural traits (such as the production of a hand axe), represent *packages* or *archives* of information transmitted across generations with more or less fidelity through cooperative activity in social groups, and cultural transmission is seen as a novel modality of information transmission, hence a major transition, according to the definition provided before.

Pavlicev *et al.* see the strong reliance on cultural transmission as the *first part* of the last major bio-cultural transition: "cultural archives in hominin history gathered together arrays of gestures involving information and interaction with material affordances of the environment" (p. 212); producing hand axes starting from a lithic core and transmitting this knowledge to conspecifics represents an example of such a logic.

"Such cultural archives had considerable power to alter the interactions of hominin groups with their environments and ultimately, through the feedback operations of niche construction, to shift the selective pressures at work on the species involved". (Pavlicev *et al.,* 2016, p. 212)

The feedback relationship between elements in play and a reciprocal causation, as well as cooperativeness, are fundamental elements, present at different levels, of Pavlicev *et al.* account.

"As hominins' cognitive capacity for shared attention grew—a growth attested in archaeologists' reconstruction of social circumstances already half a million years ago — the coordinated turn-taking of modern human discourse could begin to form. The kinds of gestures and calls that must have long characterized *protodiscourse*, partly innate and involving pointing signification, came to be more firmly tied to this coordination, and this solidified linkage altered vocalized interactions on the landscape in new, advantageous ways. The value of intensified vocal interaction and collaboration drove selection for greater control and variety in vocalization. (…) New capacities for production of the new repertories of calls but new capacities for their perception and interpretation as well. (…) The selection, in other words, was not only for communicative gesture but also for the capacity to attend to it—the very shared attention that set off the communicative changes in the first place. A feedback cycle was closed." (Pavlicev *et al.,* 2016, p. 213-214)

Pavlicev *et al.*, describe this systematization of the communication system as the *second part* of the last major bio-cultural transition, namely the transition from protolanguage forms to modern languages framed as a transition from analogical forms of communication (protodiscourse and protolanguage) to a discrete or digitalized form (today apparent both in language and in music), with a role played by new capacities for hierarchized cognition attested in the archeological record (see also Di Vincenzo and Manzi, 2013).

We would like to reinterpret Pavilcev *et al.* suggestion of splitting the last major transition in two parts, identifying more precisely (1) the first as the evolution of capacities for cumulative culture and (2) the second as the evolution of language, that is a more systematized communication system (probably relying on discrete infinity).

According to the argument developed during this work, we believe that these two steps are parts of the same major transition because the underlying evolutionary process might be shared. In particular we identify this process with the expanded version (genetic assimilation plus *cultural assimilation*) of the assimilate-stretch principle that we proposed here, an abstract evolutionary model that can stand at the bases both of the evolution of cumulative culture and the evolution of language features. In fact, as reported in fig. 5 in the Introduction, the Behavior X that complexifies in Behavior X+1 might be in principle every kind of behavior, not necessarily or strictly a linguistic feature. The assimilate-stretch principle in fact has been applied to explain cognitive evolution and more specifically categorization in non linguistic behaviors such as predator avoidance in Avital and Jablonka (2000). It might in principle work also for other culturally transmitted traits following a cultural-phenotype-first and a gene-as-followers logic. That's why we see a certain continuity between the cultural drive hypothesis and the expanded account presented here of the assimilate-stretch principle. The complexification of behaviors that might emerge according to the assimilate-stretch logic could provide a plausible process at the bases of cumulative culture; moreover, the assimilate-stretch principle was originally presented to explain the evolution of language, with which it remains consistent. We believe that the expanded account of the assimilate-stretch principle presented here might in principle be an evolutionary process that integrates biological and cultural change at the bases both of the capacities for cumulative culture (such as enhanced information processing capacities, or improved working memory) and capacities specific for language, intended as a high-fidelity transmission mechanism. In fact, it seems plausible that general features such as enhanced brain capacities for information processing (already exploited for cumulative culture) are older and more genetically modulated than specific linguistic capacities, which are arguably more recent and probably more culturally modulated: for example, the Iterated Learning Model developed by Simon Kirby and colleagues today provides a cultural explanation for syntactic features in language, without assuming a strong genetic base.

In conclusion, we think that we explored a tentative explanation for what kind of evolutionary process was involved in the co-evolution of cumulative culture and language, that we characterized here in the end of our route as two steps of the last major transition occurred in human evolution. We believe that for the tentative explanation provided, it is indispensable to rely on some of the main epistemic elements of an Extended Evolutionary Synthesis.

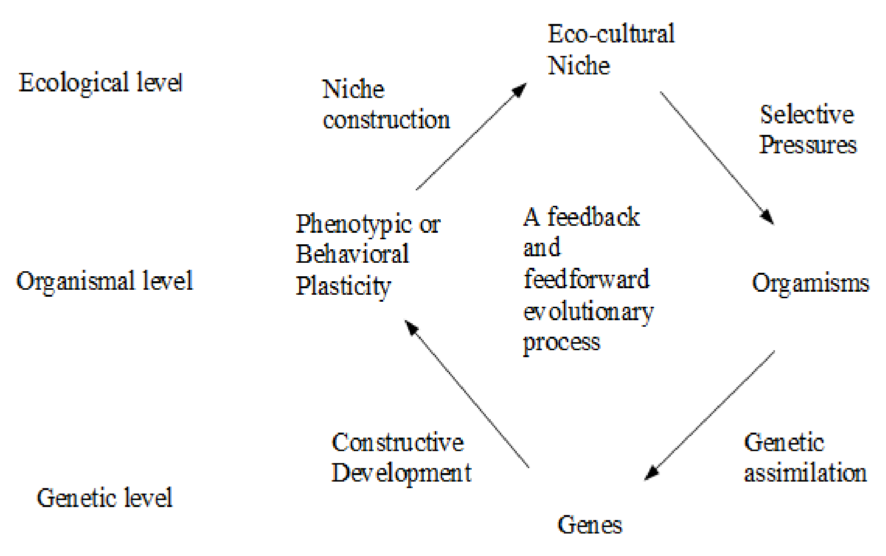

Figure 7.
here summarized the feedback evolutionary process, with interactions occurring across the hierarchical levels, described in the expanded version of the assimilate-stretch principle, with the EES main ingredients at work: niche construction, phenotypic plasticity, constructive development, genetc assimilation, feedback processes across the hierarchical levels.

Moreover, to understand the feedback dynamic in play, it is also indispensable to adopt a multilevel perspective to appreciate how entities at different levels of the biological hierarchy influence each other (see figure 7). This is why in chapter three we argued that a reciprocal causation model (see fig. 8 for a recapitulation of the feedback relationships) should be the standard model of causation in evolutionary biology, but also that it should be implemented with a multilevel perspective, allowing to appreciate upward and downward casual influences across the biological hierarchy.

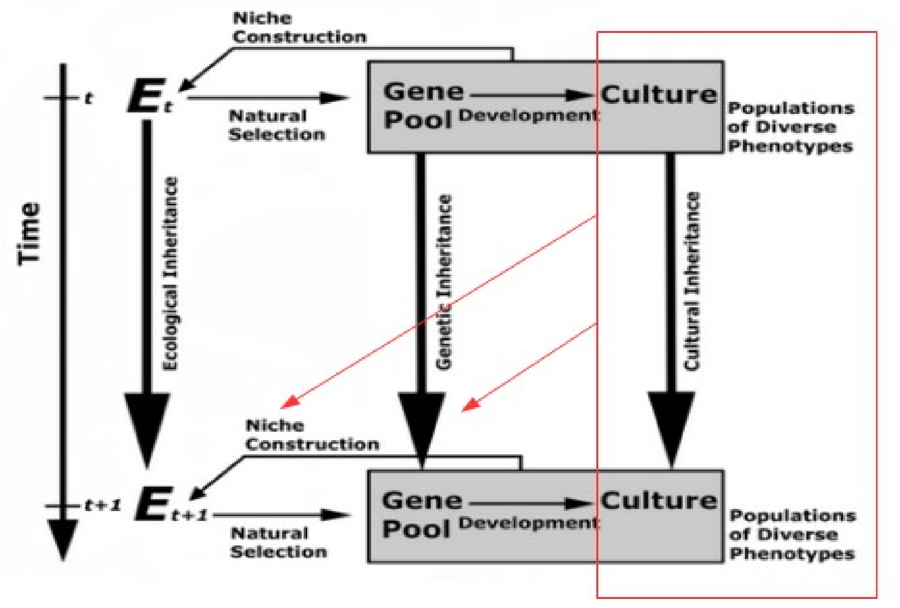

Figure 8. An inclusive inheritance perspective showing the feedback relationships between hierarchical levels (ecological, organismal, genetic) and between evolutionary processes: the biological (natural selection and niche construction) and cultural one. The transgenerational feedback role of cultural inheritance is highlighted.

Moreover we argued that an explanatory pluralism should be adopted when the evolution of a complex mosaic of traits such as language is considered. This means that it is likely that different evolutionary processes, at different evolutionary stages, are responsible for the evolution of such a complex trait. In fact, in the first chapter we argued that the initial stages of language evolution might be intended as the evolution of a form of verbal teaching between mothers and offspring (Mother Tongue hypothesis, Fitch, 2004; 2007; Laland, 2016) and hence a kin selection dynamic might have played a significant role. At later stages of language evolution, when the trait started to spread across the population, also among non-kin, a frequency dependent selection model might explain the accelerated rates of co-evolution between culture and higher-fidelity transmission mechanisms: we discussed this in chapter three (Suman, submitted) taking as a case study Morgan *et al.* (2015) experiment. We proposed here in the conclusions an expanded version of the assimilate-stretch principle as a good model capable of integrating both biological and cultural evolutionary processes, even though this proposal is still at a tentative stage here and further inquiry is required to assess under which conditions it is advantageous for genetic assimilation to occur and under which conditions it is advantageous for cultural assimilation to occur.

We believe that in principle the EES-inclined explanation we tried to provide in this work is able to integrate biological and cultural evolutionary processes and hence to overcome what we identified as some of the main difficulties of the SET approach. We believe that this represents a substantial virtue for the EES and future studies in this field cannot ignore key concepts like niche construction, inclusive inheritance, reciprocal causation in language evolution studies.

However, the analysis proposed here only argues that a theoretical framework (EES) shows to be more appropriate than another (SET) in framing a certain topic of research; future work will establish whether specific predictions can be advanced adopting this updated conceptual framework. In order to maintain that a research programme is actually an expansion of the rival one it should be shown that it is able to explain new facts with new predictions that don't rely on assumptions belonging to the rival research programme. Gene-culture co-evolutionary studies have already proved their fruitfulness not only in the domain of human behavior and human evolution but also in other non-human social species (see Foote *et al.*, 2016). A gene's eye view clearly revealed to be insufficient to shed light on human evolution, whose complex interactions go beyond the scope of a reductionistic approach; gene-culture co-evolutionary models are among the most promising approaches to tackle human evolution and we argue that the EES conceptual framework provides concepts and explanatory tools to properly do so. If in the next future new specific predictions generated within the EES conceptual framework will be empirically corroborated also in the domain of language evolution, we could testify the actual expansion in this case-study. For now the debate is still open and alive.

REFERENCES (INTRODUCTION AND CONCLUSION)

Anderson ML (2010) Neural reuse: a fundamental organization principle of the brain. Brain Behav Sci, 33:245-313

Arriaga G, Zhou EP, Jarvis ED (2012) Of mice, birds and men: the mouse ultrasonic song system has some features similar to humans and song-learning birds. PLOS ONE, 7(10): e46610

Avital E, Jablonka E (2000) Animal Traditions: Behavioural Inheritance in Evolution. Cambridge University Press, Cambridge

Baldwin JM (1896) A new factor in evolution. Am Nat, 30, 44-51, 536-53

Batali J (2002) The negotiation and acquisition of recursive grammars as a result of competition among exemplars. In: Briscoe E (ed) Linguistic Evolution through Language Acquisition: Formal and Computational Models, 111–172. Cambridge: Cambridge University Press

Beckers GJL, Bolhuis JJ, Okanoya K, Berwick RC (2012) Birdsong neurolinguistics: Songbird context-free grammar claim is premature. NeuroReport, 23: 139–145

Berwick RC, Friederici AD, Chomsky N, Bolhuis JJ (2013) Evolution, brain and the nature of language. Trends Cogn Sci, 17, 2:89-98

Berwick RC, Chomsky N (2016) Why only us. The MIT Press, Cambridge, MA

Bickerton D (1990) Language and species. University of Chicago Press, Chicago

Bickerton D (1995) Language and human behavior. University of Washington Press, Seattle, WA

Boeckx C (2014) What Can an Extended Synthesis do for Biolinguistics: On the Needs and Benefits of Eco-Evo-Devo Program. In: Pina M, Gontier N (eds) The evolution of social communication in primates, Springer Cham Heidelberg New York Dordrecht London

Boeckx C, Del Carmen Horno-Chéliz M, Mendevil-Girò J (2012) Integrating linguistics and biology. In: Boeckx C, Del Carmen Horno-Chéliz M, Mendevil-Girò J (eds) Language, from a Biological Point of View: Current Issues in Biolinguistics, Cambridge Scholars Publishing, Newcastle upon Tyne, UK

Benitez-Burraco A, Theofanopoulou C, Boeckx C (2016), Globularization and domestication. Topoi, doi:10.1007/s11245-016-9399-7

Boeckx C, Benítez-Burraco A (2014) The shape of the human language-ready brain. Front Psychol, 5:282

Boesch C (2003) Is culture a golden barrier between human and chimpanzee? Evol Anthropol 12, 82–91

Bolhuis JJ, Tattersall I, Chomsky N, Berwick RC (2014) How could language have evolved? PLoS Biol 12(8): e101934

Bolhuis, JJ, Tattersall I, Chomsky N, Berwick RC (2015) UG or not to be, that is the question, PLoS Biol, 13(2): e1002063.

Bowling DL, Fitch WT (2015) Do animal communication systems have phonemes? Trends Cogn Sci, 19, 10:555-557

Brighton H, Kirby S, Smith K (2006) Cultural selection for learnability: Three principles underlying the view that language adapts to be learnable. In: Tallerman M (ed) Language Origins: Perspectives on Evolution, chapter 13, Oxford University Press, Oxford

Bromham L, Hua X, Fitzpatrick TG, Greenhill SJ (2015) Rate of language evolution is affected by population size. Proc Natl Acad Sci USA, 112, 2097–2102.

Burling R (1993) Primate calls, human language, and nonverbal communication. Curr Anthropol 34, 25–53

Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? Trends Cogn Sci, 12, 5:187-192

Cavalli Sforza LL, Feldman MW (1981) Cultural transmission and evolution. University of Princeton Press, Princeton

Charbonneau M (2015) All innovations are equal, but some more than others: (Re)integrating modification processes to the origins of cumulative culture. Biol Theory, 10:322-335.

Chomsky N (1968) Language and Mind. New York, Harcourt, Brace.

Chomsky N (1988) Language and problems of Knowledge. The MIT Press, Cambridge (Mass).

Chomsky N (1993) A minimalist program for linguistic theory. In: Hale K, Keyser SJ (eds) The View from Building 20: Essays in Linguistics in Honor of Sylvain Bromberger (Current Studies in Linguistics 24), 1-52, The MIT Press, Cambridge, MA [Reprinted in Chomsky N., 1995. The Minimalist Program (Current Studies in Linguistics 28), 167-217. The MIT Press Cambridge, MA]

Chomsky N (2005) Three factors in language design. Linguistic Inquiry, 36, 1–22

Chomsky N (2010) Some Simple Evo-devo Theses: How True Might They Be for Language?
In: Larson R., Déprez V., Yamakido H. (eds) The Evolution of Human Language.
Cambridge: Cambridge University Press, 54–62.

Chomsky N (2012) The Science of Language. Interviews with James McGilvray. Cambridge University Press, Cambridge

Christiansen M, Kirby S (2003) Language evolution: Consensus and controversies. Trends Cogn Sci, 7, 300–307

Claidière N, Scott-Phillips TC, Sperber D (2014) How darwinian is cultural evolution? Phil Trans R Soc B, 369:20130368

Corballis M (1999) The Gestural Origins of Language: Human language may have evolved from manual gestures, which survive today as a “behavioral fossil” coupled to speech. Am Sci, 87.2, 138-145

Croft W (1990) Typology and Universals. Cambridge Univ Press, Cambridge, UK

Danchin E, Charmantier A, Champagne FA, Mesoudi A, Pujol B, Blanchet S (2011) Beyond DNA: integrating inclusive inheritance in an extended theory of evolution. Nature Reviews Genetics 12: 475-486

Darwin CR (1859) The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London (6th ed: 1872)

Darwin CR (1871) The Descent of Man, and Selection in Relation to Sex. London, John Murray

Deacon T (1997) The Symbolic Species, Penguin Books

Dean LG, Kendal RL, Schapiro SJ, Thierry B, Laland KN (2012) Identification of the Social and Cognitive Processes Underlying Human Cumulative Culture. Science, 335, 1114-1119, DOI: 10.1126/science.1213969

Dean LG, Vale GL, Laland KN, Flynn E, Kendal RL (2013) human cumulative culture: a comparative perspective. Biol Rev, 89, 284-301

Dessalles J (1998) Altruism, status and the origin of relevance. In: Hurford JR et al. (eds) Approaches to the Evolution of Language, 130–147, Cambridge University Press

de Waal FBM, Ferrari PF (2010) Towards a bottom-up perspective on animal and human cognition. Trends Cogn Sci, 14, 5: 201-207

Dor D, Jablonka E (2000) From cultural selection to genetic selection: a framework for the evolution of language. Selection 1 – 1.3, 33-55

Dor D, Jablonka E (2001) How Language Changed the Genes: Towards an Explicit Account of the Evolution of Language. In Trabant J (ed), Essays on the Origin of Language. Berlin: Mouton, 149–75

Dor D, Jablonka E (2004) Culture and Genes in the Evolution of Human Language. In: Goren-Inbar N, Speth JD (eds) Human Paleoecology in the Levantine Corridor. Oxford: Oxbow Books, 105–114

Dor D, Jablonka E (2010) Canalization and Plasticity in the Evolution of Linguistic Communication. In: Larson R, Déprez V, Yamakido H (eds) The Evolution of Human Language. Cambridge: Cambridge University Press, 135–47

Dor D, Jablonka E (2014) Why we need to move from gene-culture co-evolution to culturally driven co-evolution. In: Dor D, Knight C, Lewis J (eds) The social origins of language, Oxford University Press, Oxford, 15-30

Dor D, (2015) The instructions of imagination, Oxford University Press, New York

Dunbar R (1996) Grooming, Gossip and the Evolution of Language. London: Faber and Faber.

Dunbar R, Shultz S (2007) Evolution of the social brain. Science 317, 5843:1344–1347

Dunbar R (1998) Theory of mind and the evolution of language. In: Hurford JR et al (eds) Approaches to the Evolution of Language. 92–110, Cambridge University Press

Enard W, Przeworski M, Fisher SE, Lai CS, Wiebe V, Kitano T, et al (2002). Molecular evolution of FOXP2, a gene involved in speech and language. Nature, 418, 6900:869–872

Dunn M., Greenhill S. J., Levinson S. C., Gray R. D. (2011) Evolved structure of language shows lineage-specific trends in word-order universals, Nature, 473, 79-82

Elman JL, Bates EA, Johnson MH, Karmiloff Smith A, Parisi D, Plunkett K (1996) Rethinking Innateness: A Connectionist Perspective on Development. The MIT Press, Cambridge, MA

Enard W, Przeworski M, Fisher SE, Lai CS, Wiebe V, Kitano T, et al (2002). Molecular evolution of FOXP2, a gene involved in speech and language. Nature, 418(6900), 869–872

Enquist M, Strimling P, Eriksson K, Laland KN, Sjostrand J (2010) One cultural parent makes no culture. Anim Behav 79, 1353–1362, doi:10.1016/j.anbehav. 2010.03.009

Enquist M, Ghirlanda S., Eriksson K. (2011) Modelling the evolution and diversity of cumulative culture, Phil Trans R Soc B, 366, 412–423

Evans N., Levinson SC (2009) The myth of language universals: Language diversity and its importance for cognitive science. Behav Brain Sci, 32, 429–492

Falk D (2004) Prelinguistic evolution in early hominins: whence motherese? Behav Brain Sci, 27, 491–503

Falk D (2009) Finding Our Tongues: Mothers, Infants and the Origin of Language. New York,Basic Books.

Ferretti F (2010) Alle origini del linguaggio umano – il punto di vista evoluzionistico, Laterza, Bari

Fitch WT (2004) Kin selection and 'mother tongues': a neglected component in language evolution. In: Oller DK, Griebel U (eds) Evolution of Communication Systems: A comparative approach. MA, MIT Press, Cambridge, 275-296

Fitch WT (2005) The evolution of language: a comparative review. Biol & Philos 20:193-230

Fitch WT (2006) The biology and evolution of music: A comparative perspective. Cognition, 100, 173–215

Fitch WT (2007) Evolving meaning: the roles of kin selection, allomothering and parental care in language evolution. In: Lyon C, Nehaniv CL, Cangelosi A (eds) Emergence of communication and language, 29-51, Springer-Verlag, London

Fitch WT (2008) Glossogeny and phylogeny: cultural evolution meets genetic evolution. Trends Genet 24, 8:373-374

Fitch WT (2010) The evolution of language. Cambridge, Cambridge University Press.

Fitch WT (2011) The evolution of syntax: an exaptationist perspective. Front Evol Neurosci 3, 9:1-

Fitch WT (2012) Evolutionary Developmental Biology and Human Language Evolution: Constraints on Adaptation. Evolutionary Biology, 39:613-637

Fitch WT, Reby D (2001) The descended larynx is not uniquely human. Proc R Soc Biol Sci, 268: 1669 – 1675

Fitch WT, Hauser MD, Chomsky N (2005) The evolution of the language faculty: clarifications and implications. Cognition, 97, 179–210

Fitch WT, Huber L, Bugnyari T (2010) Social cognition and the evolution of language: constructing cognitive phylogenies. Neuron Review, 65, 795-814.

Fodor J (1983) The modularity of mind. The MIT Press, Cambridge (Mass)

Fogarty P, Strimling P, Laland KN (2011) The evolution of teaching. Evolution 65, 10:2760-2770

Foote et al (2016) Genome-culture co-evolution promotes rapid divergence of killer whales ecotypes, Nature Comm, 7:11693, DOI: 10.1038/ncomms11693

Gentner TQ, Fenn KM, Margoliash D, Nussbaum HC (2006) Recursive syntactic pattern learning by songbirds. Nature 440: 1204–1207

Gibbons A (2014) How we tamed ourselves and became modern – 'self-domestication' turned humans into the cooperative species we are today. Science, 346, 6208: 405-406

Gould SJ (1977) Ontogeny and Phylogeny. Cambridge, Harvard University Press

Gould SJ (1991) Exaptation: a crucial tool for an evolutionary psychology. J Social Issues, 47, 3:43-66

Gould SJ (1993) Eight little piggies: Reflections in natural history. New York: Norton

Gould SJ, Lewontin R (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B 205:581-598

Gould SJ, Vrba ES (1982) Exaptation – a missing term in the science of form. Paleobiology 8:4-15

Greenfield PM (1991) Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behaviour. Behav Brain Sci, 14, 531– 95

Griffin AS (2016) Innovativeness as an emergent property: a new alignment of comparative and experimental research on animal innovation Phil Trans R Soc B, 371: 20150544

Groszer M, Keays D, Deacon R, de Bono J, Prasad-Mulcare S, Gaub S, et al (2008) Impaired synaptic plasticity and motor learning in mice with a point mutation implicated in human speech deficits. Curr Biol, 18, 354–362

Haesler S, Rochefort C, Georgi B, Licznerski P, Osten P, Scharff C (2007) Incomplete and inaccurate vocal imitation after knockdown of *FoxP2* in songbird basal ganglia nucleus Area X. PLoS Biol, 5(12), e321

Hauser MD, Chomsky N, Fitch WT (2002) The faculty of language: what is it, who has it, and how did it evolve? Science, Doi: 10.1126/science.298.5598.1569

Hawkins JA (ed) (1988) Explaining Language Universals, Blackwell, Oxford

Herrmann E, Call J, Hernández-Lloreda MV, Hare B, Tomasello M (2007) Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. Science, 317, 1360-1366.

Hewes G (1973) Primate communication and the gestural origin of language. Curr Anthropol, 14, 5–25

Hillert DG (2015) On the evolving biology of language. Front Psychol, 6, 1796, doi: 10.3389/fpsyg.2015.01796

Hinton GE, Nowlan SJ (1987) How learning can guide evolution. Complex systems, 1:495-502

Hoppitt W, Laland KN (2013) Social learning – an introduction to mechanisms, methods and models. Princeton University Press, Princeton and Oxford

Hunt G, Gray R (2003) Diversification and cumulative evolution in New Caledonian crow tool manufacture. Proc R Soc B, 270, 867–874

Hurford JR (2003) The language mosaic and its evolution. In Christiansen M, Kirby S (eds) Language Evolution, Oxford University Press, Oxford, 38-57

Hurford J (2014) The origins of language, Oxford University Press, Oxford

Jablonka E, Lamb M (2005) Evolution in four dimensions. The MIT Press, Cambridge, MA

Jablonka E. Lamb M (2006) The evolution of information in the major transitions, J Theor Biol, 239, 236–246

Janik VM, Slater PB (1997) Vocal learning in mammals. Adv study Behav, 26: 59 – 99

Jarvis ED (2006) Selection for and against vocal learning in birds and mammals. Ornithological Science, 5:5-14

Kirby S (1998) Language evolution without natural selection: From vocabulary to syntax in a population of learners, Edinburgh Occasional Papers in Linguistics, 1-38

Kirby S (2002) Natural language from artificial life. Artifcial Life, 8: 185–215

Kirby S (2007) The evolution of language. In: Dunbar R, Barrett, L (eds) Oxford Handbook of Evolutionary Psychology. 669–681, Oxford University Press, Oxford

Kirby S, Hurford J (2002) The emergence of linguistic structure: an overview of the iterated learning model. In: Cangelosi A, Parisi D (eds) Simulating the evolution of language. Springer

Kirby S, Dowman M, Griffiths TL (2007) Innateness and culture in the evolution of language. Proc Natl Acad Sci, 104, 12:5241-5245

Kirby S, Cornish H, Smith K (2008) Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. Proc Natl Acad Sci 105, 31:10681-10686

Knight C (1998) Ritual/speech coevolution: a solution to the problem of deception. In: Hurford JR et al (eds) Approaches to the Evolution of Language, 68–91, Cambridge University Press

Krause J, Lalueza-Fox C, Orlando L, Enard W, Green RE, Burbano HA, et al. (2007) The derived FOXP2 variant of modern humans was shared with Neandertals. Curr Biol, 17(21), 1908–1912

Laland KN, Galef BG (2009) The question of animal culture. Harvard University Press, Cambridge, MA

Laland KN, Odling-Smee J, Myles S (2010) How culture shaped the human genome: bringing genetics and the human sciences together. Nature Rev Gen, 11:137-148

Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T (2011) Cause and effects in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science, 334:1512-1517

Laland K. N., Odling-Smee J., Hoppitt W., Uller T. (2013) More on how and why: cause and effects in biology revisited. Biol Philos, 28:719–745

Laland KN, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J, (2014) Does evolutionary theory need a rethink? Yes, urgently. Nature 514:161–164

Laland K. N, Uller T, Feldman MW, Sterelny K, Mu¨ller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282:20151019.

Laland KN (2015) On evolutionary causes and evolutionary processes. Behavioral Processes 117-

97-104

Laland KN (2016, in press) Culturing the mind, Princeton University Press, Princeton

Lewis HM, Laland KN (2012) Transmission fideliy is the key to the build-up of cumulative culture. Phil Trans R Soc B, 367:2171–2180

Lieberman P (1984) The Biology and Evolution of Language. Harvard University Press, Cambridge, MA

Lightfoot D (2000) The spandrels of the linguistic genotype. In: Knight C, Studdert-Kennedy M, Hurford JR (eds)T he evolutionary emergence of language: Social function and the origins of linguistic form. 231–247, Cambridge, England, Cambridge University Press

Lupyan G, Dale R (2010) Language structure is partly determined by social structure, PLoS ONE 5, e8559

Maynard Smith J, Szathmary E (1995) The major transitions in evolution, Freeman, Oxford

Mayr E (1961) Cause and effect in biology. Science 134:1501–1506

Mayr E (1982) The growth of biological thought – diversity, evolution and inheritance. Harvard University Press, Cambridge, Mass

Mayr E (2005) What makes biology unique. Cambridge University Press, Cambridge

Mesoudi A (2011) Cultural evolution – how Darwinian theory can explain human culture and synthesize the human science. University of Chicago Press, Chicago and London

Mivart GJ (1871) On the Genesis of Species Macmillan and Co., London

Moczek AP et al. (2015) The significance and scope of evolutionary developmental biology: a vision for the 21st century. Evolution & Development 17:3, 198–219

Motterlini M (2000) Lakatos – scienza, matematica e storia. Il Saggiatore, Milano

Muthukrishna M, Henrich J (2016) Innovation in the collective brain. Phil Trans R Soc B 371: 20150192

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN (2016) The coevolution of innovation and technical intelligence in primates. Phil Trans R Soc B, 371: 20150186.

Noël Haidle et al (2015) The Nature of Culture: an eight-grade model for the evolution and expansion of cultural capacities in hominins and other animals. J Anthropol Sci, 93, 43-70

Notthebohm F (1976) Vocal tract and brain: a search for evolutionary bottlenecks. Ann NY Acad Sci, 280: 643 – 649

Odling Smee FJ, Laland KN (2011) Ecological inheritance and cultural inheritance: what they are and how do they differ? Biol Theory, 6:220-230

Okanoya K (2007) Language evolution and an emergent property. Curr Op Neurobiol, 17, 271-276

Okanoya K (2012) Behavioural Factors Governing Song Complexity in Bengalese finches. International Journal of Comparative Psychology. 25, 44-59

Okasha S (2006) Evolution and the levels of selection, Oxford – New York, Oxford University Press

Okasha S (2011) Emergence, hierarchy and top-down causation in evolutionary biology, Interface Focus, doi:10.1098/rsfs.2011.0046

Pagel M (2012) Wired for culture – the natural history of human cooperation. WW Norton & Company, USA

Parravicini A, Pievani T (2016) Continuity and Discontinuity in Human Language Evolution: Putting an Old-fashioned Debate in its Historical Perspective. Topoi, DOI: 10.1007/s11245-016-9431-y

Pavlicev M, Prum RO, Tomlinson G, Wagner GP (2016) Systems emergence: the origin of individuals in biological and biocultural evolution. In: Eldredge N., Pievani T., Serrelli E., Temkin I. (eds) Evolutionary theory: a hierarchical perspective. The University of Chicago Press, Chicago, 203-223

Petkov CI, Jarvis ED (2012) Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. Front Evol Neurosci, 14, 12: 1 – 24

Pievani T (2011) An evolviong research programme: the structure of evolutionary theory from a lakatosian perspective. In: Fasolo A (ed) The Theory of Evolution and Its Impact. Springer-Verlag, Berlin, 211-228

Pievani T (2013) Anatomia di una rivoluzione – la logica della scoperta scientifica di Darwin. Mimesis, Milano - Udine

Pievani T (2015) How to rethink evolutionary theory: a plurality of evolutionary patterns. Evolutionary Biology, DOI 10.1007/s11692-015-9338-3

Pievani T. (2015b) Filosofia della biologia. In: Cambiano G, Fonnesu L, Mori M (eds) Problemi d'oggi, Il Mulino, Bologna, 177-190

Pievani T, Serrelli E (2011) Exaptation in human evolution: how to test adaptive vs exaptive evolutionary hypotheses. J Anthropol Sci, 89:1-15

Pinker S, Bloom P (1990) Natural language and natural selection. Behav Brain Sci, 13 (4): 707-784

Pinker S (1994) The Language Instinct. Harper Perennial Modern Classics, New York, NY

Power C (1998) Old wives' tales: the gossip hypothesis and the reliability of cheap signals. In Hurford, JR et al. (eds) Approaches to the Evolution of Language, 111–129, Cambridge University Press

Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? Behav Brain Sci. 1, 515–526

Ramus F, Fisher SE (2009) Genetics of language. In: Gazzaniga M (ed) The cognitive neurosciences. The MIT Press, Cambridge, MA, London, England, 855-872

Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci USA, 99, 4436–4441

Reader S, Laland KN (2003) Animal innovation. Oxford University Press, Oxford

Reader SM, Hager Y, Laland KN (2011) The evolution of primate general and cultural intelligence. Phil Trans R Soc B, 366, 1017– 1027

Rendell L, Boyd R, Cowden D, Enquist M, Eriksson K, Feldman MW, Fogarty L, Ghirlanda S, Lillicrap T, Laland KN (2010) Why copy others? Insights from the social learning strategies tournament. Science, 328(5975):208-13, doi: 10.1126/science.1184719

Rizzolatti G, Arbib M (1998) Language within our grasp. Trends in Neuroscience, 21, 188–194

Savage-Rumbaugh S et al (1998) Apes, Language and the Human Mind*,* Oxford University Press

Scott Phillips TC (2015) Speaking our minds, Palgrave Macmillan, New York, NY

Scott Phillips TC, Kirby S (2010) Language evolution in the laboratory. Trends Cogn Sci, 14:411-417

Simpson GG (1973) The Baldwin effect. Evolution, 6, 342

Spierings MJ, Ten Cate C (2016) Budgerigars and zebra finches differ in how they generalize in an artificial grammar learning experiment. Proc Natl Acad Sci, doi/10.1073/pnas.1600483113

Steels L (2006) Experiments on the emergence of human communication. Trends Cogn Sci 10, 347–349

Somel M, Rohlfs R, Liu X (2014) Transcriptomic insights into human brain evolution: acceleration, neutrality, heterochrony. Curr Op Gen & Dev, 29, 110-119

Stotz K, Griffiths P (2011) Genetics and Philosophy. An Introduction. Oxford University Press, Oxford

Suman F, Pievani T (2015) The evolution of human language: an alternative scenario. Paradigmi Rivista di Critica Filosofica, 2:173-196

Suman F (2016) An updated evolutionary research programme for the evolution of language. Topoi, doi:10.1007/s11245-016-9419-7

Suman F (submitted) Integrative and separationist perspectives: the causal role of cultural transmission in shaping the language-ready brain. Biology & Philosophy

Suzuki TN, Wheatcroft D, Griesser M (2016) Experimental evidence for compositional syntax in bird calls. Nature Comm, 7:10986, DOI: 10.1038/ncomms10986

Szamado S, Szathmary E (2006) Selective scenarios for the emergence of natural language. Trends Ecol Evol, 21, 10: 555-561

Theofanopoulou C, Boeckx C (2015) Cognitive phylogenies, the Darwinian logic of descent, and the inadequacy of cladistic thinking. Front Cell Dev Biol 3: 64, doi:10.3389/fcell.2015.00064

Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Phil Trans R Soc B, 364, 2405–2415

Tinbergen N (1963) On aims and methods in ethology. Zeitschrift fu¨r Tierpsychologie 20:410–433

Tomlinson G (2015) A Million Years of Music: The Emergence of Human Modernity. New York: Zone Books

Van Schaik CP, Burkart JM (2011) Social learning and evolution: the cultural intelligence hypothesis. Phil Trans R Soc B, 366, 1008–1016

Van Schaik CP, Isler K, Burkart JM (2012) Explaining brain size variation: from social to cultural brain. Trends in Cognitive Sciences, 16, 5: 277-284

Waddington CH (1957) The strategy of the genes: a discussion of some aspects of theoretical biology. Allen & Unwin, London

Wallace AR (1869) Sir Charles Lyell on geological climates and the origin of species. Quarterly Review, 126 (252): 359-394

Wallace AR (1870) The limits of natural selection as applied to man. In: Wallace A. R. Contributions to the theory of natural selection. A series of essays. Macmillan, London

Weissengruber GE, Forstenpointner G, Peters G, Ku¨ bber-Heiss A, Fitch WT (2002) Hyoid apparatus and pharynx in the lion (Panthera leo), jaguar (Panthera onca), tiger (Panthera tigris), cheetah (Acinonyx jubatus), and domestic cat (Felis silvestris f. catus). J Anat (London) 201: 195 – 209

White SA, Fisher SE, Geschwind DH, Scharff C, Holy TE (2006) Singing mice, songbirds, and more: Models for FOXP2 function and dysfunction in human speech and language. J Neurosci, 26(41), 10376–10379

Wray A (1998) Protolanguage as a holistic system for social interaction. Lang Comm, 18(1):47-67

Wilson AC (1985) The molecular basis of evolution. Sci Am, 253, 4, 164-173

Wyles et al. (1983) Birds, behaviour and anatomical evolution. Proc Natl Acad Sci USA, 14:4394-7

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