ON THE ROLE OF HUMAN ONTOGENESIS IN THE EVOLUTION OF LANGUAGE

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Abstract

The place of organismal development in evolution is a matter of spirited debates among competing evolutionary paradigms. The Extended Evolutionary Synthesis(EES) attributes crucial role of epigenesis, i.e. the process of interaction of genes and environment at a molecular level by which the environment guides the spatial and temporal expression of genes in the formation of the biological body. Moreover, it states that epigenetic processes influence the trajectory of evolution by altering genomic expression. In essence, evolution of the phenotype is better explained as evolution of developmental mechanisms. And these are guided by the environment as a selective agent for the phenotype and behaviour.

At the same time humans are species highly influenced by culture and learning which makes culture a decisive component of the environment as adaptive factor for human development.
Students of the evolution of language have argued for a strong influence of human ontogeny in the evolution of language although schools of thought diverge as some focus on epigenetic processes in phylogenesis of the language faculty while others explore the role of language learning in cultural and social contexts in glossogenesis of linguistic diversity.

The article argues that through language-gene co-evolution some key aspects of language, learned anew at the very first stages of language origins, eventually alter the developmental mechanisms and become instinct-like predispositions, incorporated into a language faculty. In this way the very essential and universal aspects of language become relegated to nature, while the idiosyncrasies of language systems continue to be learned and evolve subjected to social and cultural influences. Notably, learners of different ages contribute differently to the evolution of language.

Keywords: evolution of language, language faculty(LF), Baldwin effect, evo-devo, Extended Evolutionary Synthesis (EES), epigenesis, ontogenesis, iterated learning

1. Introduction: ontogenesis and its role in phylogenesis in the history of evolutionary thought

Ontogenesis, i.e. the development of the individual organism from birth to maturity, and its role of phylogenesis ,i.e. evolution of species, has a long and checkered history. It has its beginnings in the philosophical debate between idealism and functionalism in ancient philosophy and has manifested in the debate between structure and function in the study of biological form. For example structuralists explain the body architecture of vertebrates with a universal body plan, or *Bauplan,* while functionalists focus on the utility of body morphology (Amundson, 2005, 2008). An evolutionary aspect of biological form through individual development predates *The origin of species* in late 19th century and is associated with the name of the structuralist Richard Owen and his conceptualization of *analogy* , i.e. similarity in body structure of distantly related species is explicable with similarity of function, and *homology,* similarity of form in species with common origin are explicable with modifications of the universal Bauplan. The study of embryology was initiated by structuralists in early 19th century with the formulation of laws of embryonic development , e.g. in early stages of embryonic development in related species embryos display morphological simplicity and similarity, which in later stages develop complexity and diversify. Species are identified in terms of common patterns of embryonic development and common adult morphology. Darwin's revolutionary idea of a tree of life explicable with descent with modification and selection channels Owen's views of development into *evolutionary morphology,* which argues that modifications of the ancestral biological form during ontogeny leads to the diversity of the adult form, marking the beginnings of the evo-devo approach(Amundson, 2005, 2008).

To sum up, the 19th century evolutionary theory views changes in biological systems as inheritance from the adult predecessor plus embryological developmental in the new generation. The interest in ontogeny as a factor in evolution was short-lived and dissipated with the proliferation of the MS and its gene-centric perspective.

1.1. Evo-devo in the Modern Synthesis (MS)

The discovery of the gene and the proliferation of Mendelian genetics, which was transformed into MS marks a crucial turn in the understanding of evolution. It has become the dominant theoretical paradigm in evolutionary biology during the 20th century. The classic understanding of evolution dominated by Modern Synthesis(MS) features the gene as the ruler of the biological universe and gene mutations as the only explanation for evolution of life on earth. Significantly, in MS the genome is conceived as a sum total of individual genes and diversity of life forms is viewed as differences in gene combinations, i.e. life is engineered by the selfish gene and its goal of self-preservation.

In MS epigenesis is an afterthought as it defines heredity strictly in terms of genetic inheritance and views epigenesis as genetically predetermined, immutable and universal process.

A version of MS, termed population genetics, defines evolution as change in genetic frequencies within a population. It introduces concepts, *genetic hitchhiking, genetic drift, founder principle, gene flow.* Genetic hitchhiking happens when a gene frequency in a population changes due to pertaining to a chromosome which is selected for its adaptive value. Gene flow is defined as migration of genes from one population to another as a result of migration of individuals. Population genetics has important contributions to understanding evolution by designing mathematical models for calculating probability of gene distribution in populations.

To note, natural selection, genetic drift and gene flow are evolutionary mechanisms which interact as each contributes to evolution. In Darwin's theory variation is a product of accidents in large populations, while variation produced by genetic isolation and genetic processes in finite populations are constrained by the specifics of the gene pool of each population. Genetic drift and similar intra-population processes could potentially neutralize or counter the effects of adaptation by fixation of deleterious genetic material(Andrews 2010). Nevertheless, organisms in all circumstances, individually and in populations, are subjected to environmental selective forces. In this sense evolution is understood as a unidirectional process of organismal adaptation to the environment in terms of the dichotomy of proximate and ultimate causes

(Mayr1961) undermines the role of development in the formation of the phenotype.

That said, the dominant status of the gene has been questioned and criticized by various authors given that in biology pleiotropy (a single gene influences multiple, often unrelated phenotypic traits) is the rule, not the exception given that a change in a single gene most often than not has no significant effect on a trait, suggesting that the genome is inherited as a whole .This explains the fact that, although mutations occur quite frequently, organisms of the same species end up remarkably similar and this is because a damage in a gene is repaired by " this amazing system for maintaining the integrity of the DNA "(Jablonka, Lamb, 2005,p. 86) Moreover, identical twins, i.e. individuals with identical genomes, differ phenotypically, and these differences emerge extragenetically, suggesting that the genome cannot be the sole mechanism determining heredity(for a summary see Bonduriansky, R. 2012). In addition, all cells in an organism inherit the same genetic information and yet they develop into specialized tissues and organs, very different in structure and function, e.g. skin, liver, etc. They follow developmental schedules, specific for the type of cells.

From evolutionary perspective this suggests that the genome evolves as a whole, not as a sum of individual evolutions of single genes. Most importantly, this reveals that the role of a single gene can only be understood through its integration and interaction in the context of the genome as a whole. In addition, it was found that " rates of molecular and morphological evolution are largely decoupled", i.e. " Phenotypic mutation rates and genetic mutation rates are dramatically different" (Skinner, Nilsson 2021, p. 1-, see also references).

Significantly, it is well known that some genes have not changed for millions of years and the same genes are found in species vastly different from one another. Humans share some genes with mice and yet, they don't have the same effect in us as in mice. Significantly, humans share about 99% of the genotype with chimpanzees, but display vastly more complex behaviour. So, even to the outside observer with no expert knowledge it is noticeable that the genome is not all that is inherited and not all that is in the genome is heritable information. It is now known that the genome is a mixture of various types of genetic material and only a small part of it codes for proteins while the rest has no role in the formation of the biological body and, thus, does not participates in evolution. In addition, beyond the genome other components of the cell are inherited and participate in the building of the phenotype, which is formed by multiple vehicles of inheritance, which affect development at different times and to different degrees as they interact(Jablonka, Lamb, 2005). This makes the role of genes and other inheritance systems and phenotypic characters difficult to evaluate.

" ...there is really no chance of predicting what (the organism) will be like merely by looking at their DNA. " (Lamb, Jablonka, 2005,p. 67)

Thus, the genocentric paradigm, or MS faces empirical challenges, suggesting that the blanket understanding of mutations as genetic accidents, blind to functionality appears to be too simplistic as " the nature of inheritance in different traits and taxa (is) spanning along a continuum from purely genetic to purely non-genetic "(Bonduriansky, 2012, p.334).

1.2. The EES a new perspective on evolution

After a long hiatus the debate on structure vs. function was reinvigorated. In this context the phenotype, i.e. the organism, identified as the unit of selection, evolves is internal balance among many interconnected components of the organism acting as a unity. This prompted the argument for a theoretical extension and conceptual enrichment of the MS, and introducing EES, acknowledging the influence of new factors and mechanisms in evolution, e.g. epigenesis, or embryonic growth, development, learning and behaviour. And the interest in evo-devo was revived.

The contributions of EES to the evolutionary theory also include acknowledgement of learned behaviours as a contributing factor as another dimension in the overall evolutionary process. As per Lamb and Jablonka (2005) inheritance of behaviours contributes to the survival advantages of individuals and influences the survival or at least the quality of life of and with it a superior reproductive potential. Crucially, evolution of adaptive behaviours often results in permanent change in the phenotype by evolution of new morphological properties(Brakefield, 2011).

EES as an extended and enriched theory of evolution also acknowledges the role of the environment in diversification of life forms, as the environment shapes the organism as much as the organism shapes the environment, first acknowledged by Lewontin (1983, 2002).The interrelation of three factors, the genotype, the phenotype and the environment, acts as a complex eco-system whose components influence each other, given that species are adapted to specific facets of the environment, i.e. environmental niches and the relationship between species and their niches is by-directional: species adapt but they also alter the environment simply with their normal metabolic processes. Thus, the organism is an active participant in its own evolution as the environment and life forms form an integrated complex, the components of which evolve in tandem by a process of co-evolution, i.e. a reciprocal evolutionary change. In fact,"...Taken together the relations of genes, organisms and environments are reciprocal relations in which all three elements are both causes and effects. Genes and environment are both causes of organisms, which are, in turn, causes of environments"(Lewontin, 2002 p.100). In short, evolution is a process of interaction of multiple inheritance subsystems, i.e genome, epigenesis, learning, environment, or evolutionary dimensions in constant interaction where "Something like evolution can occur in each dimension. But...we are not made up of four neat and separate dimensions, we are a messy complex. And it is the complex that evolves " (Lamb, Jablonka, 2005, p. 231). In sum, evolution is a multidimensional process integrating multiple levels and mechanisms of inheritance.

1.2.1. Ontogenetic development and the EES

Reinterpretation of key concepts in evolutionary theory was prompted by a number of recent discoveries(Amunson, 2005, 2008), e.g. *homologous genes,* found in species of very different taxa, separated by millions of years of evolutionary time, operating on developmental processes, was found to be crucial for the phenotypic diversity of species. For example, the Pax6 gene was found to be highly similar at bio-chemical level in insects and mice which operates on development as it stimulates translation of other genes into phenotypic traits. Crucially, its functions differ in different species, e.g. it is a participant in building different types of eyes in different species. The discovery of the Hox genes, which attach to a chromosome and control the development of segmentation of the biological body, e.g. head, torso, extremities, etc. is the same in insects, vertebrates and humans, revealed that the building of a body is beyond the exclusive control of the gene as defined by the MS. Thus, a fine-grained understanding of genetics in terms of molecular sequences lead to advances in understanding of the gene beyond their identification with individual phenotypic characters.

In addition heritable information is contained beyond the genes at cellular level, e.g. the DNA molecule is only one component of the cell structure, along with RNA and other molecules, which contain information about the building of the phenotype, i.e the cell is inherited as a whole. The cell functions by cooperation of different types of molecules and multicellular organisms function by cooperation of multiple cell types. Thus, cooperation, not competition, is at the foundation of life. The same sequences of DNA are integrated, or " packaged" differently in different cell groups dependent on their function in the production of the phenotype . Cell memory includes information on patterns on activation of gene function through regulatory genes which regulate the timing and location of turning on/off of gene functions during development as different DNA sequences are activated at different times and chromosome locations, i.e. information on cell development is also heritable.

In this sense intracellular bio-chemical processes reveal the crucial role of epigenetics in phylogeny. This triggered a new understanding of the evolutionary process and the status of the genes as dependent of extragenetic interpretation by developmental processes which afforded the empirical support and the conceptual framing of embryological development, prompting a revival of interest in its role in the building of the biological body.

The term *epigenesis* was coined by Waddington in the 1940s and refers to processes of formation of the phenotype, through interaction of the genome with the environment at the molecular level. Epigenetic mechanisms " regulate genomic activity independent of DNA sequence"(Skinner, Nilsson 2021, .3), therefore, genomic activity is conditioned on epigenetic processes. The environmental influence on gene activity thorough epigenetic processes produces variation at the level of cells, organ tissues and morphology. Temperature, stress, nutrition, even the sun, etc. are environmental factors trigger epigenetic response, although epigenetic processes can be triggered by organism-internal and intracellular factors as well. The epigenetic routines are also referred to as canalization as they constrain and shape and trajectory of the developmental process to follow established pathways (Jablonka, Lamb, 2005 and elsewhere). The term *canalization* was introduced by Waddington to mean reliable preservation of developmental routines by insulating these from possible perturbations caused by environmental or other influences. The term d*evelopmental plasticity/phenotypic plasticity* stands for the ability of an organism to alter its phenotype by altering of ancestral developmental processes in response to environmental changes without participation of genes, i.e. biological innovations are produced by evolution of development beyond the genome. Epigenesis is poorly understood and controversial topic and its role of epigenesis in evolution is actively debated.Epigenesis is poorly understood and controversial topic and its role of epigenesis in evolution is actively debated as its adequate understanding is hampered by obstacles both theoretical and experimental. As Burggren (2016) explains, on the one hand epigenesis is regarded in digital terms as presence vs. absence of a trait, while in fact epigenetically derived traits become detectable not in the first but in successive generations of offsprings and thus are counted as absent, especially in species with long lifespan for which developmental data is not accessible. In addition, epigenetic routines are not uniformly preserved as in some species the effects of epigenesis dissipate with time. Thus, epigenesis displays complexity and irregularities not accounted by theoretical instruments. Epigenetic

routines are subjects to evolutionary processes and a growing number of scholars recognize that most epigenetic changes are preserved over time, i.e. they are heritable and affect multiple successive generations and have the potential to affect evolution, which justifies arguments for the conceptual integration of epigenesis into the evolutionary theory. In this sense, as per the proponents of EES, epigenetic mechanisms are active participants in the overall evolutionary process on par with genes (Jablonka, Lamb, 2005).
To note, as per Skinner, Nilsson (2021) epigenetic changes are five times more frequent than genetic mutations, suggesting that epigenesis has crucial role in variation and adaptation, crucial for evolution. That said, although epigenesis can be effective adaptive response to environmental fluctuations, as per Burgeren (2016) this may not always to be the case as in rapidly changing environments today's beneficial epigenetic adaptations may suddenly become counter-adaptive in a new environment.

The focus on development is articulated by the Developmental Systems Theory (DST) (Griffiths, Hochman, 2015) in its approach to evolution and inheritance. The unit of selection in the theory is the life cycle as a process of development and its replication as it determines the viability of the adult organism. DST attributes the formation of the biological form to phenotypic plasticity where the environment influences changes in the biological organism which in turn alters the genetic makeup, i.e. the causality is reversed from phenotype to genome through development, i.e. genetic mutations are the result, not the cause. Similarly, West-Eberhard (2003)argues that phenotypic novelties are generated with the mutual accommodation of genotypic and environmental factors interacting during development. Moreover, the theoretically established dichotomy between genes and environment, and the characterization of the genome as the controlling factor of development and genetic mutations as the only source of phenotypic diversity, is rejected as misleading, given that different phenotypes are produced by the same genomic information where the same environmental signals are read and interpreted differently by the individual developmental mechanisms, i.e. variation is created by development. In this context the genome is redefined as " potential resources for developmental pathways, rather than fixed pieces of information" (Sultan, 2017, p.6) and the attention is focused on developmental plasticity under environmental conditions, or eco-devo. A relatively recent summary of the evo-devo agenda in its quest for understanding the evolution of biological form can be found in Breakfield (2011)
Diversification of species by epigenetic variation can explain evolutionary puzzles inexplicable by Mendelian genetics. A well-known example of the role of epigenetic influence on the genome is the Baldwin effect.

1.2.2. From learning to genes: Waddington and Baldwin

In current biological thought , dominated by the MS perspective on evolution, Lamarckian perspective, featuring a role for learning in genetic evolution, is consistently rejected.
A less popular alternative, which lately has increasingly gained influence, argues that behaviours initially learned, where learning is used in a very broad sense of acquiring a behaviour without genetic input by taking advantage of developmental plasticity, could eventually become fixed by instinctive response. The argument for genetic assimilation of acquired behaviours as a factor in evolution, known as Baldwin effect, named after J. Baldwin, states that behaviour, which initially consumes much effort and time to learn, can gradually

become easier to master with every new generation to the point when very little or no learning is required and the behaviour essentially becomes instinctive. In short, " natural selection can convert what was originally a learned response to the environment into behaviour that is innate." (Jablonka, Lamb, 2005, p.285).

Under the Baldwin effect learning can reveal hidden genetic potential and take advantage of it by altering the genome via exposing hidden genetic variation to selection e.g. in domestication of animals. In a similar vein Waddington's argument for genetic assimilation of learned behaviours reveals that a large part of the genome is dormant or not participant in evolution. In this sense genetic assimilation is achieved by internal reorganization of the genome, revealing the huge potential of underused genetic variation. In this process genes and alleles, initially neutral to adaptation, are recruited for a new function of supporting a new instinct and made available for participation in evolution as they are exposed to selection.

Some recent studies have brought new attention to Baldwin's argument and highlighted its focus on development in evolution(Jablonka, Lamb, 2005) arguing that normal evolutionary processes of variation and selection work on epigenetic mechanisms , i.e. epigenetic processes also evolve. Some are triggered by accidental copying errors in gene replication, in others, environmental factors can influence the epigenetic processes directly, e.g. environmental changes, especially high levels of stress may cause deviation from the normal direction of canalization. For example in Waddington's experiments with Drosophila (1953) external stressful conditions applied repeatedly result in deviation form the normal pattern of development. Significantly, the argument stipulates that once the organism adapts to the new environmental conditions by altering its developmental routines, even if these environmental pressures are no longer in place, the new developmental pattern will be preserved for various generations and inherited by the new generation of Drosophila, a process termed " genetic assimilation of acquired characteristics". Epigenetic mechanisms are by definition non-genetic and thus, not Mendelian, e.g. Waddington's experiments with Drosophila, where a new morphological trait is developed without genetic input.

To note, in Baldwin genetic assimilation is not a direct inheritance of learned behaviours, i.e. Baldwin effect is different from Lamarck's hypothesis which argues for direct conversion of behaviour, learned by parents, into behavioural instinct in descendants.

Epigenetic changes are preserved over generations, i.e. they are heritable and affect multiple successive generations. Importantly, developmental mechanisms can also impose selection pressures on variation by imposing selection biases on morphology and in this way influence the trajectory of evolution, which justifies arguments for the conceptual integration of epigenesis into the evolutionary theory(see Laland et all. 2012 for a review).

Waddington's study of Drosophila challenges the argument for the unidirectional nature of information transfer from genotype to phenotype as it shows that extra- genetic developmental factors cause alterations of the genome through alteration in the functions of regulatory genes, causing " reverse translation", i.e. the phenotype does influence and trigger changes in the genome. Most recently, challenging the genocentric argument that genes remain unchanged, unaffected by development, Jablonka and Lamb show(2005 chap. 2. p. 68) that genes often become altered as a normal response by feedback form development. The immune system is one example, where genes responsible for producing antibodies become altered in various ways in response to the environment. The point here is that the information in the genome does not always becomes faithfully copied but is subjected to interpretation and often edited during development under environmental influences(Caroll, S.2005). Developmental patterns are both stable and flexible, e.g. they are faithfully inherited by canalization, while at the same time more flexible and adaptable than the genome, i.e. more open to evolvability. Baldwinian evolution illustrates an intelligent solution nature can take advantage of in order to successfully respond to unpredictable environmental challenges.

To clarify, Waddington shows that environmental conditions can alter the development of biological properties, while Baldwin argues for internalization of learned behaviours, and even learning directed by consciousness, i.e. Baldwin hypothesizes will and choice as a factor in evolution(Downes 2003). A detailed comparison of Waddington's and Baldwin's contributions to evolutionary theory can be found in Crispo 2007.

Notably, it is useful to clarify the term “innate” and “ internalized” here stands for properties which develop regularly and uniformly with minimum input from the environment, be it by direct genetic encoding, bio-chemical triggers as in epigenesis, i.e. embryonic growth, or neuronal networks formed within the brain by input from experience, as in development. A stable environment is a prerequisite for genetic assimilation to take place , as in fast changing environments learning is adaptively advantageous. Only the simplest and most general aspects of behaviour are assimilated. The transition from learning to instinct also implies that the behaviour becomes universally represented in all individuals. And if some part, usually the most stable part of a behaviour becomes instinctive, this opens possibilities for more learning and consequently, increased behavioural complexity.

As illustrated by Avital, Jablonka (2000), learning happens in various ways, e.g. by trial and error of the individual learner, by observation and imitation or instruction by conspecifics (social learning), or a combination of both. Individuals learn differently deploying individual learning strategies and it is difficult to find generalized patterns in individual learning. In social learning, on the other hand, the same information is learned, producing the same neuronal representation in the brains of learners and the teachers, producing a universal pattern of neuronal pathways in all members of the population. In this sense one is to suspect, after Avital and Jablonka(2000) that the learning patterns formed by repeated practices of social learning are more likely to be internalized given the universality of brain processes and pathways involved.

It is argued that internalization of learned behaviours has both advantages and disadvantages, e.g. while genetic facilitation for learning is adaptive in stable environments, learning plasticity is adaptive in environmental variability, learning is a costly investment given the time and energy involved. On the other hand, fixing in the genome a previously learned behaviour is adaptive as it eliminates phenotypic variability, i.e. delivers phenotypic uniformity and decreases energy cost (Sznjder, et all. 2012). At the same time replacing learning and thus, flexibility with internalization, understood as limiting learning flexibility, is viewed by some as a detriment to adaptability (Weber, Depew, 2003). In this sense Baldwinian processes reveal nature's compromise: a spectrum of innateness and environmental adaptability.

“ In between these extremes lies a spectrum of outcomes where traits contain a genetic component, but they are also to various degrees modifiable in response to environmental influences” (Sznajder et all. 2012, p. 301).

To sum up, genetic and epigenetic inheritance interact as two interdependent processes which often cannot be separated.

It is noteworthy to remember, that the Baldwin effect is currently a hypothesis and given the scarcity of empirical evidence in its support , the status of the Baldwin effect in evolutionary theory is thus far unclear.

1.2.3. Evo-devo, reciprocal causality and niche construction

Species are adapted to specific facets of the environment, i.e. environmental niches. The attention to the role of the environment in evolution was pioneered by Lewontin (1983, 2002) who argues argues organisms exist and function as a part of a larger organization, the environment, with which they interact, i.e. that an organism is not separable from its environment. Moreover, the two are intertwined, the environment shapes the organism as much as the organism shapes the environment. The interrelation of three factors, the genotype, the phenotype and the environment, acts as a complex eco-system whose components influence one another and change in coordination. In other words, there is *reciprocal causation* and the evolutionary process is multidirectional(Laland et all. 2012 and elsewhere). The genome, development and environment are co-dependent and co-evolving as interacting agents in a triple helix (Lewontin 2002). Through their very functioning biological bodies trigger environmental changes which act as selection pressure, inducing adaptive responses in descendants, affecting their development, i.e. development happens in context. Developmental routines are perpetuated over generations, thus affecting phylogenesis by providing " environmentally contingent repertoire of potential phenotypes" (Sultan, 2007, 2017). As framed succinctly by Sultan " Phenotypes are produced actively through the process of individual development, as shaped by the genotype's interactions with regulatory information that is conditioned by past and present environments"(Sultan, 2017, p.22).

Organismal changes triggered by this interaction can be genetic, developmental, behavioural. One of the most widely cited example of niche construction is the formation of dams as " beaver aquatic adaptations in response to beaver-generated aquatic niche"(Deacon, 2009, p.3). The resulting evolutionary innovations are often initiated at behavioural level and can potentially be inherited by developmental mechanisms, given the inherent phenotypic plasticity and adaptive potential and evolvability of developmental pathways. Some developmental innovations become incorporated into the genome, making their replication permanent and universal, although more often than not adaptation is accomplished without genomic changes, given that the genome is highly stable and conservative and resists change.

For hominids and especially for humans culture forms integral part of the environment and its influence on human evolution e.g. control of fire, domestication of plants and animals , etc. have triggered evolution in digestion, resistance to diseases, termed by some as " ecological inheritance", initiated by development(see Laland et all. 1996; 2012, and elsewhere; Richerson, Boyd, 2005). Importantly, the ubiquity of these interactions, repeatedly demonstrated by growing number of empirical findings, earns their place among the theoretical instruments of evolutionary biology by extending the conceptual arsenal accordingly.

3. Evo-devo in biolinguistics

The generative / biolinguistic approach defines the evolution of language in terms of biological growth of the language faculty as part of the general growth and maturation of the human body, a position articulated in detail in well-known works of Chomsky, Bickerton, Pinker and others. Under this approach the content of the language faculty and the process of its biological growth were viewed as genetically controlled developmental instinct, an approach rooted firmly within the MS and focussed on FOXP2 gene as the grammar gene(Gopnik et all.1996). In subsequent transformations of the biolinguistic paradigm e.g. the Principles and Parameters focuses on the phenotype as it identifies two types of language -dedicated cognitive resources, FLN and FLB(Hauser,Chomsky, Fitch 2002 and elsewhere). By postulating a set of genetically determined principles and binary sets of parameters, where the universal properties of languages are attributed to the principles and the observable diversity of languages is explicable with variation in combinations of parameter settings, activated during ontogenetic development, i.e. acknowledging a role for development in the growth of the language faculty (FLN). In this context the gene-centred perspective of the MS is maintained as *Evo-Devo gen,* despite allowing for some environmental influence by turning on a developmental program upon exposure to a local language. In the latest version of generativism, the Minimalist agenda(Chomsky, 1995; Hauser et all. 2002 and elsewhere) the role of genes is significantly reduced and a major role is attributed to symbol learning which by its nature is subjected to cultural evolution. A useful discussion of the evo-devo approaches and their understanding of biology, genetics, development and evolution in the formation of the LF can be found in Benitez-Burraco, Longa 2010. The minimalist agenda in its proposal of three factors in the formation of the LF , relinquishes the genocentrism of earlier stages as it further reduces the role of the genetic endowment to some unspecified capacity for recursion and attributes significant role to learning in language attainment and , by extension, in the evolution of language as behaviour, a view essentially consistent with the theoretical fundamentals of the usage-based paradigm and acknowledged by Hauser, Chomsky, Fitch (2002). In this sense the evo-devo agenda in the generative/ biolinguistic approaches displays internal controversies in its understanding of biology, genetics and development and their role in the formation of the LF.

An interesting speculation on the role of development, understood as hybridization of genetic endowment and communicative experience in the formation of I-language comes from Balari, Lorenzo(2018 and elsewhere), stipulating that the normal growth of UG is actively and continuously stimulated by experience at every step, analogue to any other instance of growth of biological and/or cognitive organs and systems across species. The development of morphological systems in languages is pointed at as a demonstration of such process of hybridization by absorbing elements of the environment into the growth and formation of the adult state of I-language as the developmental target.

In sum, although the biolinguistic understanding of the growth of the LF has changed over time by acknowledging a role of developmental factors, for the majority of scholars it remains within the frames of MS as it maintains a genocentric view.

4. Beyond biology: the development of language by enculturation

4.1. Evolution of human culture as a Darwinian process

Although it is common for scholars to automatically adopt the conceptual machinery of MS as

instrument for understanding evolution of human culture, the mechanics of these two processes differ significantly. For example:
a. Learned behaviours are not transmitted genetically, while cultural innovations acquired during life time are inherited directly by the next generation, i.e.biological evolution is Darwinian-Mendelian, cultural evolution is Lamarckian.
b. In biological evolution the genomes of the parents are inherited in their entirety at the single point of conception, while cultural inheritance happens piece-meal at different points of the learning process.
c. Cultural inheritance is mediated by social interaction during learning as conscious behaviour, while genes are inherited directly, by instinctive urge to produce offsprings.
d. In genetic transmission the offspring has no active role in the production of the new genotype, while in cultural inheritance the learner is active participant by making choices in reflection of one's individuality.
e. In life forms an organism inherits characteristics of two parents, while in cultural inheritance multiple community members , e.g. parents, extended family, neighbours, teachers etc. are contributors.
f. In life forms genetic variation is produced by recombination of the pool of parental genes, while the learner is also an active participant and can introduce his/her own innovations, in this way contributing to cultural diversity.
g. In biological evolution the biological survival in the environment is the selection factor, while in cultural context the social and cultural environment is of primary importance.
h. Cultural evolution is much faster and flexible than biological evolution, which makes it more adaptive in response to environmental challenges, which makes culture a much more significant adaptive force in human evolution, than genetic evolution. See Waring, Wood (2021) for discussion.

A gene-centred model of biological evolution is taken by R. Dawkins (1976) as a theoretical platform for understanding cultural evolution. He identifies the " meme" as the unit of cultural transmission , defined as a unit of information analogue to the gene, as a replicator where minds are vehicles, multiplying individual memes by imitation/learning.

" Cultural transmission is analogous to genetic transmission in that, although basically conservative, it can give rise to a form of evolution. " (Dawkins, 1976, e-book v1.0. , p. 169).

As an alternative Claidiere et all. (2014) propose adopting a population thinking in modelling cultural evolution and define culture by analogizing propagation of cultural behaviours and artifacts via learning by imitation to transmission of infectious diseases, i.e. epidemiological phenomenon within a population. In this context a cultural entity, e.g. an idea, behaviour, a linguistic form, etc. invades a population of minds. In addition, the minds in the culture-hosting population and the cultural entity, i.e the invader, co-evolve.

D.Hull has gone even further with the generalized theory of evolutionary change which abstracts the evolutionary principles from their original biological context and applies them to understand change of any entity in any field, hence the label Universal Darwinism. At the foundation of Universal Darwinism are the basic principles of Darwinian evolution : **a.** replication by which evolving entities are multiplied, **b**. variation produced by copying errors during the replication (Darwin's descent with modification)**c**. competition among the variants fulfilling the same function , **d**. selection leading to differential retention of some variants and the elimination of others, based on superior survivability under current circumstances. The theory is applied for explaining changes in various spheres : life forms, cultural practices, from technology, farming, fashion, to institutions, language. In analogy to the gene-centric theory of biological evolution, Hull understands the universal evolutionary process in terms of dichotomy of genotype and phenotype as two different entities with two different roles in it. The universality of the evolutionary process is signalled by the abstract notions 'replicators' (the containers of information which is copied , analogue to genotype)and 'interactors' (entities which interact with the environment and are subjected to selection, analogue to phenotype), although the theoretical alliance with biology is maintained by clarifying that, like in biology, the roles of replicators and interactors can be assumed by different entities at different levels of structural complexity. For example, genes, chromosomes and species can be both replicators and interactors. A detailed analysis of Hull's theory can be found in Croft 2013, p. 11- .

In sum, despite similarities, biological evolution and cultural transmission are different processes, accomplished by different mechanisms, suggesting that theoretical frameworks of biological evolution should be used only broadly and with caution for understanding cultural processes.

4 .2. Glossogenesis(evolution of languages) as a cultural process

The formation and perpetuation of individual language systems is a cultural process, thus, the mechanics of cultural evolution are expected to apply in the study of glossogensis. In linguistics there is a long tradition in defining language diversity in biological terms as diversification of languages from a common ancestor. It begins with Darwin himself who has written about the analogy of languages to species(Darwin, 1871) a tendency continued by 19th century European linguists. With the discovery of the genome and reinterpretation of Darwin's theory in terms of Mendelian genetics the traditional analogy of language and biological forms has been reinterpreted by finding analogies with genes and linguistic forms.

In contemporary linguistic theorizing principles and methods of modern genetics are borrowed into linguistics by usage-based approaches in effort to understand change in language systems as linguistic forms are likened to genes and language systems to genomes . In historical linguistics concepts from genetics are applied for determining the ancestral roots of languages as branches of language families. In this way the phylogeny of populations is stipulated to be analogue to the glossogenesis of languages as the principles of evolution by variation, inheritance and natural selection are used metaphorically to explain the shape of modern languages in terms of adaptation to historical and cultural changes.

Others adopt E. Mayr's population view of organisms, i.e., a population perspective defines languages in therm of a population of idiolects(Mufwene 2014 and elsewhere) e.g. two language varieties are considered the same language if people can successfully communicate, thus, they speak the same language. In analogy to species' reproductive isolation as the cause of speciation, communicative isolation leads to loss of intelligibility and language diversification, i.e. a language is defined in terms of the communicative interactions in a population of speakers. For example in Croft (2000) language is a pool of linguemes, analogous to a population, which exist and replicate in coordination, i.e. as parts of a larger entity. No distinct levels of complexity are proposed in life forms and in ideas, which, as evolving entities, are defined not by the nature of its replicators, but by the nature of their interactors and their interactions. The replicators are nested in structures of ever growing complexity such as phonology, syntax, morphology. The replication of a phoneme requires coordinated replication of other phonemes and the replication of linguistic forms, similarly, requires the coordinated replication of other such linguemes, i.e. the language system changes as a whole. Linguemes have variants, e.g. alternative phonetic realizations of a phoneme, synonyms of words and constructions, etc. The linguemes in a language are formed by linguistic conventions.

In Croft's model glossogenesis/language change displays the distinctive features of evolution:

A. variation : variation in various levels of language use is pervasive: 1. there is diversity of idiolects, 2. among sociolects, as sociolinguistic diversity, motivated by various social factors: age, gender, class , 3. variation within idiolects : in phonetics, lexicon and grammar as the same person is found to use different linguistic devices at different occasions in expressing the same idea.

B. competition : two or more vocabulary items are used as alternatives to encode the same concept, i.e. synonyms of various types of constructions,from lexical words to grammatical forms, are alternatively used to describe the same event .

C. inheritance : as utterances are used in communication they replicate the features of linguemes and some linguistic forms are persistently passed on , which makes possible understanding between generations, and texts written centuries ago allow historical linguists to determine language families**.**

D. selection: language change /glossogenesis is a process by which some linguemes are used more often than others and replicated disproportionately at the expense of others. In this context, although the theoretical perspective of population genetics stipulates that changes in biological and cultural systems are oblivious to selection, in Croft a search for superior expressivity, avoidance of ambiguity and misunderstanding results in preferential use as selection factor.

Further, a version of the Developmental Systems Theory is adopted as the evolutionary process of replication and selection of linguistic items is understood as happening in cycles, e.g. an instance of use of a linguistic item, (an utterance, a word, etc.) forms a cycle, starting with an abstract idea, a concept conceived in the mind of the speaker, is emitted and perceived in material form by the mind of a hearer where it ends up again as a concept, marking the end of the cycle. Thus, an idea is copied/replicated from one mind into another, where as in biological evolution, variation is produced during the copying process(Croft, 2000 chap.2, p. 24).

4 .3. Language learning as symbol inheritance

As an alternative scholars espousing the usage-based spectrum of perspectives understand language learning by youngsters as a result of exposure to a rich environment of social and cultural activities, or *enculturation(* Griebel, Pepperberg, Oller, 2016), where language is learned with bio-cognitive properties, already present in various pre-human species and mostly preserved in the human lineage. The uniquely human abilities to learn language are attributed to " self-organized emergence" (ibid.p. 435) from interaction of pre-human cognitive abilities and elevated developmental plasticity under the crucial influence of training and enculturation. In this sense key aspects of language, e.g. semanticity, displacement, functional variability, demonstrated in various illocutionary uses, combinatoriality and symbols as unique features, in contrast to alarm calls and human non-linguistic signals, emerge by observation and active participation in social and cultural interaction with conspecifics. Moreover, words label experience in a situation -independent way and refer not only to parts of reality but also to each other, i.e. a word is used in combination with other words and knowledge of a word implies knowledge of the possible word combinations in which it is likely to participate. The lexicon is a mixture of lexical words with concrete meanings, grammatical words with general meanings and linguistic forms which occupy the grey area in between, forming a continuum. Languages evolve by changing the place of linguistic forms along this continuum. The theory of grammaticalization (Hopper and Traugott. 2003 and elsewhere) identifies the process by which some lexical items with high frequency of occurrence acquire structural properties, i.e. become grammaticalized and outlines a trajectory of the typical path of transformation from a lexical item to grammatical form in terms of change in category, i.e. lexical (content) word>grammatical word> clitic>inflectional affix. The process of grammaticalization encompasses semantic, followed by structural and phonemic alterations and involves usage expansion, generalization of meaning or ' bleaching' and reduction or complete loss of independence to the point of becoming a morpheme, and reduction of the phonological form. The change is unidirectional from lexical to grammatical, completing the universal life cycle where linguistic forms exist, live, change in form and function and disappear. In this context language evolution is cycles of grammaticalisation, each enfolding in the minds of youngsters during language learning and further perpetuated .Thus, languages evolve as they are learned.

4 .3.1. Iterated learning of language

The learning of linguistic symbols by each new generation is viewed as a type of inheritance, during which language systems are also reinvented. This is captured by the Iterated Learning framework, which points at the crucial role of ontogenesis in the formation of compositional language, understood in evolutionary terms as a continuous process of regularization and structure formation as adaptation of the language system to learnability(Smith, Kirby, Brighton, 2003 and elsewhere).The hypothesis is empirically demonstrated with language games featuring artificial agents as interacting communicators, where from initially holistic flow of speech linguistic structure emerges by formation of lexical categories, e.g. NP (Noun Phrase), VP (Verb Phrase), etc. and grammatical categories, e.g. tense, aspect, etc. (Kirby, Griffits, Smith, 2014 and elsewhere). The formation of structure is accomplished with the support of resources mimicking the cognitive abilities of human learners and understood as coordinated species-specific but not language-specific. The emergence of compositionality is understood here as a solution to bottlenecks, formed when a large volume of traffic attempts to go through a narrow passage causing blockage or delay in the flow, which results in reorganization in the flow. In the context of language learning a bottleneck is defined as the inability of the artificial "mind" to absorb the wealth of samples of natural language to which it is exposed during the period of language learning. The problem is solved by compressing the flow of information by selective attention to simple and regular forms, easier to absorb by underdeveloped minds, resulting in introduction of structure. Such bottlenecks are said to be essential for emergence of compositionality and of grammatical rules.

The experiments of the Iterated Learning Hypothesis on artificial agents show similar results upon observations of young children during early language development, e.g. language learning starts with holistic utterances which gradually become parsed into smaller combinable units (Tomasello in Givon 2002, p. 310-)

From evolutionary perspective the linguistic regularities, introduced by young minds during language learning are said to be preserved and inherited over generations, each contributing additional regularity to the language system. That said, although the artificial agents' tendency to simplify and streamline linguistic forms by introducing regularity and compositionality are corroborated by human toddlers' linguistic behaviour, e.g. goed vs. went, comed vs.came, these don't become adopted by the population at large and fade away as over- regularization becomes just a short phase in the child's language development and thus, is not likely to have lasting influence in the evolution of language systems.

4.4. Iterated learning, a developmental process of structure formation in knowledge representation

The proponents of the usage-based approaches attribute language-relevant functions to a number of cognitive properties of which language takes advantage and shares with other human behaviours, e.g. general learning and participation in culture (Kirby, 2017 and elsewhere). This suggests that compression and generalization of all types of knowledge is organized and transmitted by the same general process of iterated learning, which makes language not different from any other learned behaviour and language learning not different from any other form of learning. And some of these suggestions are confirmed by experiments, e.g. human semantic memory contains some universal categories, represented by dichotomies of animate vs.inanimate, human vs. non-human, singular vs. multiple, close vs. distant , presence vs. absence, instantaneous events vs. processes of long duration, measurable vs. unmeasurable substances, etc.,(Dor Jablonka, 2000, p.39-)which can be interpreted as the tendency of the human mind to represent knowledge of reality in a compressed and structured way. Significantly, these universal frames of categorization come naturally to young learners, suggesting innate aspects for the fundamentals of human thought. And these universal patterns of categorization are identified as a common semantic core consistently reflected in the grammatical systems of all languages.

Moreover, cognitive capacity for processing structured behaviour in cognition and praxis, a phenotypic expression of various genes (Dediu, Levinson, 2018) most prominently FOXP2, is involved in the formation of the human basal ganglia, instrumental to the ability to dance, produce and manipulate tools, and speech and language, demonstrating the innate link between language use and extralinguistic activities. (Liebermann, 2000, 2016 and elsewhere) These seem to be the same cognitive mechanisms hypothesized by Lotem et all.(2017) evolved for data processing into structured packages in co-adaptation of brain and culture.

To note, iterated learning is not unique to humans as it is demonstrated by bonobos and some birds, displaying commonalities in cognitive predispositions for learning and socialization and suggesting commonalities in cultural evolution by simplification and compression of knowledge , although we humans are unique in the diversity and complexity of behaviours transmitted by iterated learning (Kirby 2017).

Thus, the human organism has evolved general mechanisms for representing and processing structured knowledge and behaviours as innate predispositions for culture, and language is merely taking advantage of these.

5. The evolution of language as evolution of language development

5.1. Language development in non-humans and humans, a comparison

In the context of the evo-devo agenda the human innate predispositions for language are a product of gradual internalization of some previously learned aspects of language by altering the epigenetic developmental mechanisms from interactions of culture with the human organism, demonstrated by the ability of young humans to master in record time and with little exposure some of the basics of language. This is not to deny or diminish the crucial role of learning in achieving adult language competence, which in usage-based approaches is identified as the crucial factor made possible by enculturation, i.e. the unique environment of social interactions within rich cultural context. (Kirby 1998; Chater, Christiansen 2009 and elsewhere).

That said, various non-human species have demonstrated learning abilities, resulting from extensive enculturation and training if raised in human families, especially at young age. (Griebel, Pepperberg, Oller, 2016). And the lack of atmosphere stimulating language learning is pointed at as the explanation for the lack of language-like communication in the wild in species with bio-cognitive attributes highly similar to humans', while the presence of rich stimulating environment explains the spontaneous language-approaching communication of parrots and cross-fostered apes, i.e. raised in human families along with children.

At the same time non-human language learners remain stagnant at learning some essential, but very rudimentary aspects of language while human learners, after an initial stage comparable to non-humans', advance rapidly and ultimately achieve full language proficiency culminating at the adult level. This significant diversion from non-human language learning suggests that human developmental mechanisms have evolved innate predispositions for the essentials of language which, coupled with extensive learning flexibility and memory capacity, has produced the human language learning mind. In this sense one would anticipate that at the onset of language it was learned by reliance on general learning capacities, implemented for learning of any new behaviour, and after multiple cycles of learning over generations and in conjunction with the development of ever more complex culture, Baldwinian processes have altered human development by converting some of the crucial features of language into innate predispositions . In this way memory space for further learning of the semantic and grammatical idiosyncrasies of languages which continue to be learned.

5.2. Evolution of human ontogeny: Baldwin effect and the evolution of a faculty for language by extension of culture to biology

A number of cognitive and physiological properties, demonstrated during early development universally across populations, are difficult to explain except as innate predispositions, evolved for language learning. A number of such predispositions are discerned.

* *a human Theory of Mind,* i.e. a capacity for anticipating communicative intention and communicative relevance as ability to participate in dialogues ,which allows for ostensive communication , i.e. participation in dialogues by Grician principles of conversation to include expectation of relevance in linguistic communication (Sperber, D. Wilson D. 2004 and elsewhere ; Scott-Philipps, T. 2017)

* *capacity for speech*. Although genetic influence on cognitive abilities is difficult to demonstrate, anatomy and physiology offers clearly demonstrable examples. The supralaringeal vocal tract in humans has a unique configuration, e.g. it is composed of two tubes positioned at 90 degrees, each of almost equal length, the human tongue has a unique shape and position in the mouth, the speech organs have unique physiology, they are very flexible, allowing rapid production of maximally distinct vocal signals, used in speech . In addition it has been argued that humans have evolved species' specific breathing control, tied to speech production. The evolution of speech involves the descent of the larynx and the descent of the tongue root (see Liebermann 2000, 2007, 2008; Fitch 2010).

An evolutionary explanation for the anatomy and physiology of the human vocal tract is only plausible as adaptation to articulate speech as it is counter-adaptive for basic biological functions, creating the potential for choking. Speech capacities demonstrate innate predispositions as the biological growth of the human vocal tract is inevitable as is the growth of all biological organs, suggesting some genetic participation. The shape of the adult human vocal tract shows similarities in Neanderthals, suggesting some form of speech, although the human articulation of quantal vowels shows unique adaptation for advanced articulatory dexterity (Liebermann, 2008 and elsewhere). Liebermann (2007) has argued that human speech capacities are the result of Darwinian processes combining anatomical and neurological alterations by genetic mutations and exaptation of preexisting structures. Thus, in human anatomy and physiology the biological function is shared with the communicative one , suggesting that they are in accord with the evolutionary principles which prefer slight gradual changes in old structures to biological novelties. Liebermann detects such changes in the basal ganglia, which affords a capacity of the brain to regulate the vocal tract's ability to form complex vocal gestures, possibly the same ability also regulating aspects of cognition and syntax, as it involves the recombination of primitives and formation of structures, suggesting that speech capacities have evolved as part of a language capacity. It is reasonable to expect that speech capacities have co-evolved with a preexisting language, i.e. human cognition has evolved to process discrete sounds and their combinations in addition to articulatory precision in articulation of discrete sounds and syllables. Such abilities could have evolved through language-gene coevolution by gradual incorporation of previously learned behaviour into human anatomy, physiology and cognition, mediated by development, i.e. by Baldwinian evolution. Moreover, the basal ganglia, identified as “ the sequencing machine “ of the brain, participates in various neural circuits in regulating coordinated movements in speech, dancing and other behaviours unique to humans, suggesting an expanded coevolutionary scenario between the genome and cultural practices beyond language (Liebermann 2000 and elsewhere).

* *infant babbling,* a developmental instinct as training of the articulatory apparatus for speech by mimicking the speech production of adults (J. Hurford, 2012)

“ The disposition to babble is thus adaptive in a social group that already benefits from communication in speech. It seems likely that a capacity for finer tuning of the articulators and more precise coordination of their interaction evolved biologically as the benefits of well articulated speech emerged. This would have been a case of gene-culture, more specifically gene-language, co-evolution.” (Hurford, 2012 p. 488).

The human innate ability for speech sound perception suggests evolution of human development as adaptation to language learning. For example, infants discriminate speech form non-speech sounds (music), and also differentiate between voiced and unvoiced consonants, suggesting that the fetus' auditory experience begins in the uterus and helps shape auditory biases demonstrated after birth(Muller R.A.1996). Animal perception shows some capacities for speech perception in some birds, monkeys and apes, suggesting evolutionary continuity.

* *a critical period for language learning*, when proficiency in a first language is achieved in early age within less than a decade by imitation and participation in communicative events (Hurford 1991; Hurford and Kirby1999).

* *some guiding principles for word formation and learning* (Bloom 2000), e.g. a child demonstrates intuitive knowledge that a word is a label for a whole object, as opposed to a part of an object, and demonstrates affinity for learning words which name whole objects, the child also appears to know without explicit instruction that there is one-to-one correspondence of words and objects, i.e. a mutual exclusivity bias. Moreover, as per Bloom (2000) children intuitively know that words are vocal signs with meanings and phonological properties which form part of a larger system, i.e. words are Saussurean signs.

* *a human capacity for symbol formation and symbolic reference* (Deacon,1997, 2009), a cognitive capacity to form complex combination of various types of referential relationships, e.g. among symbols as members of a symbolic system, between a symbol and its referent, and among objects in reality as perceived by the human organism. It is viewed as a product of evolution of development, in adaptation to cultural evolution of symbolic from motivated signs and the evolution of language as a part of niche construction. In addition, the neurological patterns of vocalizations were altered to permit the production of speech.

**a unique human cognitive niche* encompassing human intelligence, sociality and language, which by co-evolving, arguably have shaped the human brain and mind. Most significantly, here the coordinated evolution of these cognitive abilities explains the evolution of the language faculty as Universal Grammar (Pinker 2010).

**integrated neurobiological mechanisms for processing the language system and language use* (Pulvermuhler, 2005, 2018) as learned words are stored in memory as rich descriptions of individual examples of use during specific events of communicative exchanges, where linguistic properties are combined with extralinguistic details in terms of detailed description of individual perceptual experiences(R. Port, 2007), implicitly positioning language within a broader environment of social interactions and extralinguistic context, i.e. as part of a human socio-cultural niche.

And given the assumption that a form of language emerged as learned behaviour and predated the evolution of the language faculty, it is reasonable to speculate that the above listed universal properties could have started as linguistic innovations, initially passed on by learning, and with time gradually become easier to learn with each successive generation.

To clarify, complex behaviours usually do not become completely instinctive, the simplest and the most stable aspects of behaviour are internalized. Partial internalization frees cognitive space for more extensive and more complex learning , resulting in increased behavioural sophistication. The presence of innate predispositions for language does not impede the learnability of linguistic properties produced by language diversity and change. In this way the successful learning of language quickly and reliably is assured by internalization of its essential properties, which frees more space in the memory for more extensive learning, for example of a larger vocabulary, grammatical forms produced by grammaticalization, etc.

In short, although general learning abilities and socialization do play significant role, the human organism has evolved some innate predispositions demonstrated by developmental biases tailored for the specific task of language learning, i.e. human development has evolved for language learning.

5.2. The co-evolution of genomic processes, human development and glossogenesis within a socio-cultural niche: eco-evo-devo and iterated learning

An environmental niche for humans includes the artificial environment constructed by invention and dissemination of cultural products, e.g. ideas, artifacts and practices, which interact and co-evolve with the human organism by mutual adaptation and reciprocal causation (Richerson, Boyd, 2005 and elsewhere; Laland et all. 2012; O'Brien, Laland 2012).

The recognition of the interaction and interdependence of nature and nurture, biology and culture, and the role of human development as a mediator of this process, advocated by the EES, is gaining influence among students of language evolution. This integrative approach does not postulate biological inheritance of linguistic features, only the ability to anticipate, learn and process such features, ability resulting from the integration of genomic and epigenetic processes, iterated learning mechanisms and the socio-cultural environment incorporating social structures and cultural conventions (Segovia-Martin, Balari 2020), i.e. the evolution of language is understood in the context of a human bio-cultural niche, constructed out of co-dependence and co-evolution of three inheritance pathways : genes, development and culture.

Importantly, cultural evolution enfolds much faster than biological evolution, suggesting that only the most stable and universal aspects of human language, listed above, would be singled out and subjected to internalization, therefore underscoring the critical role of socio-cultural processes during ontogenesis of language.

5.2.1. Language learning and social structure

Language is learned within a social context. In this sense the observable correlation between the type of social organization is interpreted by Croft (2003) as more than mere coincidence, but as co-dependence. The types of language systems discussed below are argued to be born by the socio-economic circumstances which determine the communicative demands of the communities.

A. Band is a closed community of about 25 usually genetically related individuals. The band's social organization is biologically defined: leaders are elders; it is an economically and politically egalitarian society, no division of labour, no permanent leadership, and no class differences. Bands have no fixed territory which is why in case of conflict do not fight, but disperse. Band economy is based on hunting and gathering. Communities have limited knowledge of the environment and as a consequence, little new information to communicate and thus, little appetite for linguistic innovations. This is the social organization, presumed to have fostered the initial stages of language formation, i.e. small vocabulary, limited grammar, monolingual society. Migration and territorial dispersion results in language divergence and formation of new languages as a result of territorial, genetic, cultural and communicative isolation.The concept of band is close to Givon's “ society of intimates”(Givon, 2002)

B. A tribe has larger population size of several hundreds and even thousands of members with relatively sedentary lifestyle and occupy a fixed territory and often enter into conflicts with neighbouring tribes as they compete for land. Economically and politically it is egalitarian society i.e., there are no class divisions and no division of labour. The economy is based on domestication of animals and plants. The population is divided into clans based on family ties which leads to competition for leadership. Knowledge of the environment is broadened, reflected in increased vocabulary size and some grammatical complexity by introducing new grammatical categories, although their use is optional .

C. Chiefdoms represent a major change in social organization. The population numbers reach multiple thousands with emergent social stratification. Permanent leadership and a ruling elite emerges based on biological inheritance and as a result class division of rulers and ruled is formed. Division of labour is represented by emergence of trades, e.g. manufacturers, builders, etc.. The population occupies and defends permanent territory, divided in villages with the chief's village having a special role as a centre of power, thus there is stratification of territory. Sophisticated social structure brings rich social relations, reflected in language as increase in vocabulary, social stratification and division of labour results in the formation of registers and registerial diversity, increased number of speakers leads to increased regularization in the language system. This implies increased role of grammar and fully modern languages and, in some cases, the formation of writing systems. Language is enriched with perlocutionary acts as its sphere of use is extended in literature, poetry, theatre.

D. States have large populations of hundreds of thousands, even millions, occupying vast territories and highly complex social organization, based on territorial integrity and class membership, which explains multiple and diverse sources of power and wealth. States are organized around a central government which results in establishment of standard dialect on which government documents are written. Social diversification and the emergence of class systems becomes reflected in sociolinguistic variation in languages systems. The centralization of power and wealth brings the ability to conquer new territories and populations thus creating multiethnic and multilingual societies. The development of trade brings long-distance travel and development of trade pidgins, migration brings multilinguism, the formation of lingua francas.

To note, the 4 types of social organizations are identified as abstract concepts as none of them is represented in pure form in any of the societies known to anthropology.

“ the range of social organizations that is actually found represents more of a continuum than a sharp division into four or so types “ (Johnson, Earle , in Croft, 2003, p. 6).

And language is learned within a context of social organization, which one may view as part of a socio-cultural ecosystem (Mufwene 2014) where language exists and adapts to the communicative demands of human societies and evolves to reflect human history. Each generation of language learners are initiators and driving force by shaping successive stages in the language system and ultimately language evolution.

5.2.2. The formation of Pidgins and creoles, a reflection of human history

Language diversity and variation in the language systems is in part explicable with language contact or lack of it, which depends on social factors, e.g. size of the community(small vs. large), the nature of the social interactions (dense or intense vs. loose) and the degree of contact (extensive vs. isolation)(Trudgill (2009). A well known example of influence of language contact on language systems is the formation of pidgins and creoles, simplified versions of modern languages born out of unusual social circumstances where speakers of modern mutually unintelligible languages must communicate. Some emerge in historical circumstances of slavery and colonization when varieties of West European languages spoken by the European traders and colonizers and the conquered populations must communicate, others are formed in trade relations. In the process a highly simplified language-like system is formed with limited communicative power, designed haphazard, to cover only the most basic communicative needs. Pidgins are concocted as a mixture of linguistic forms of both language systems, generally striped of grammatical features to bare stem, with a small lexicon where words are arranged in sequence by semantic principles. Creoles are more complex with some grammatical devices and larger lexicons. Mufwene (2007, 2009)regards the emergence of pidgins as a case of " language restructuring " or " system reorganization", triggered by language contact in unique historical circumstances. In this sense pidginization is an attempt of anatomically modern and cognitively normal adult speakers of modern, but mutually unintelligible languages, to invent a maximally simplified, although useful in the circumstances, communication system. Pidgins start as not fully systematic, given that the I-languages of the speakers, which are fully systematic, have not had sufficient time to converge " in ways observable in language varieties of stable communities , where mutual accommodations have made the idiolects more similar to one another, a stage demonstrated by the formation of creoles "(Mufwene, 2009.p.7)

In short, historical and cultural upheavals, i.e the socio-cultural ecology, are absorbed , perpetuated by the young generation who reinvent the language system to reflect these changes making their contributions to language evolution.

5.2.3. Cultural values are reflected in language systems through language learning

Formal theories regard culture irrelevant in the formation of linguistic systems, understood as representation of universal properties of human cognition. That said, field studies contradict this common assumption. A case study by D.Everett of Piraha, a language spoken by a small tribe in Brazil demonstrates the influence of culture on linguistic structure. Pirahas live and think in the present, believing that the present is a repetition of the past which will be repeated in the future and this is why communication is restricted to immediate experience, i.e they avoid talking about knowledge of experience beyond immediate past.

" Grammar and other ways of living are restricted to immediate experience, (where experience is immediate in Piraha if it has been seen or recounted by a person alive at the tale of telling)" (Everett,

2005. p. 622).

Pirahas have no myths or folktales about their history which explains the lack of past tense or any other grammatical devices for marking past events. Moreover, Piraha language lacks numerals and grammatical number or other ways of encoding quantification which correlates with the lack of concepts for precision and counting. They often indicate quantity by gesturing the distance between the hand and the ground. Piraha is also a language without colour terms and has the smallest inventory of pronouns and the simplest kinship system. Interestingly, Piraha lexicon has no words for individual fingers and refers to fingers as " hand sticks". Pirahas often point not with the fingers but with the jaw, lip, or motion of the head. There is no word for " last". Piraha language also lacks embedding, both phrasal and sentential . It has the smallest phoneme inventory which differs by gender, e.g. women have inventory of seven consonants and three vowels, men have eighth consonants and three vowels. As a compensation Piraha language makes extensive use of prosody and other non-verbal vocalizations, e.g. whistling, singing. Pirahas are monolingual and despite opportunities for close contacts with Brazilian people are not interested in learning Portuguese language or anything about the world beyond. In sum, Pirahas live in a present extended to infinitum and young learners absorb and perpetuate the world view, cultural values and the language system of a community resistant to change.

In other studies a relation of elements of grammar , e.g. the use of subordinate clauses, are explained with appearance of literacy and narrative. An example is the case of clause subordination in Greek, absent in Homer's oral poetry, but clearly present in the classic Greek literature and philosophy(as discussed by Newmeyer, in Wray, 2002, p.369). Similarly, Givon (1979) explains detailed linguistic structure with the influenced of culture through literacy and finds that the languages of pre-literate societies are organized by pragmatic principles based on information structure e.g. loose word order, topic and focus marked by stress, little to no morphology, while the grammars of English, Greek, etc., languages with long literary traditions display structural detail and sophistication, e.g. subject-predicate structure , strict word order, morphology, phrasal and sentential embedding. Thus, it is argued that changes in culture, i.e. the invention of writing and literacy, triggers changes in the language systems, which are perpetuated by generations of language learners through schooling and education.

The argument for causal association of literacy and the structure of languages is challenged as some languages, e.g. Chinese with a long history of literacy, despite preserving its reliance on pragmatic principles, while some languages spoken by pre-literate societies in Africa display subject-predicate structure and complex syntax. Obviously, the relationship of language systems and culture is complex. In short, linguistic interactions and innovations are dependent on a number of socio-cultural factors, specific to the individual communities, their cultural idiosyncrasies, social structure and historical circumstances as part of a socio-cultural niche. The socio-cultural environment and its changes are absorbed and perpetuated by young learners who channel the language system to reflect these changes.

6. Perspectives on language development in contemporary linguistic thought

6.1. A language faculty emergent during development

In contemporary linguistic thought, mostly influenced by the generative understanding of language attainment, termed as acquisition, knowledge of language is viewed inherent the architecture of the human brain and encapsulated by a bio-cognitive module specialized for language processing, i.e. the Language Faculty(LF), which attains its adult form by the general principles of biological growth during early stages of human development. The nature and functions of the so hypothesized bio-cognitive entity is said to be genetically inherited and develops top-down, i.e. from genotype to phenotype and behaviour, in uniform succession of stages of growth. Significantly, the development of the LF is said to be largely insulated from experience.

Alternatively the emergentist paradigm within the usage-based approach argues that at birth learning mechanisms are simple and general and specialized neuronal organization is emergent and experience-dependent. MacWinney (1998)points out that “children learn language gradually and inductively, rather than abruptly and deductively. There is little evidence for a tight biological timetable of developments of the type that we see in other species... it is impossible to find evidence for some discrete moment at which a child sets some crucial parameter...it is very difficult to use standard experimental methods to prove that children have acquired some of the abstract categories and structures required by Universal grammar” (MacWinney, ibid. p. 1).

The emergentist perspective explains the cognitive aspects of language emergence as not different from any other complex behaviour by making use of more primitive cognitive abilities, e.g. perception, motor control, concept formation, generalization. MacWinney (1998 p. 7) describes the learning of lexicon as emergent association of three types of neuronal maps in three areas of the cortex : concept map, articulatory map and auditory map. R.A.Muller elaborates :

“ Language areas’ develop epigenetically. They are the end products of complex chains of interactions with internal and external environments. These interactions are probabilistic events based on, but not rigidly determined, by the genome… ‘Innateness’ or genetic determination applies to a relatively high degree to basic principles of brain organization, such as : maturational schedules…It applies to a very limited degree only to the functional organization of higher cognitive functions, including language… The organization of linguistic knowledge therefore results from linguistic processing. Or, in linguistic terms, language competence in the adult speaker can only be explained in terms of language processing and performance in the child. There is no particular cytoarchitectonic design in the (left) persylvian cortex specifically destined to assume language functions.” (R.A. Muller, ibid. 6.3.).

Ellis (1998) argues that ruled behaviour in general and rules in linguistic communication, in particular, emerge as patterns in the human mind post-genetically as part of the development of the phenotype. So what is inherited is not rules but pathways of control over the gene functions at particular stages of development of the organism.

Behaviourally the process works by starting small with short and simple expressions, gradually adding more complex forms and structures. For example all children begin their first experience with language by experimenting with a few isolated lexical words and articulating clumsy one-word utterances, whose meanings are highly ambiguous and context-dependent. Later children gradually combine two or more lexical words into simple phrases before producing full sentences(Tomasello 2005 and elsewhere).

In this sense, as per the emergentist argument individuals differ in their experience with language and each individual applies their own unique strategies in language learning as both words and grammatical rules are learned in a variety of ways , and thus, represented differently in different minds. From this one would infer that each individual mind constructs its own version of LF, contradicting the generative argument for uniformity of language acquisition. Thus, there are as many language capacities as there are individuals, although these must be highly similar to make communication possible.

6.2.1. The hypothesis for critical period in language acquisition

Under the current status quo the individual's development is genetically controlled and follows strict time schedule. This includes a critical period, a hypothetical window of opportunity during which species, capable of learning are innately predisposed for fast and effective learning of a skill. For humans proficiency in the native language is thought to be attained most successfully during the critical period, estimated to end at puberty. In biolinguistic context the critical period for language acquisition is a genetically controlled process of biological growth and maturation of LF in the first few years of life, which at puberty is turned off, making the acquisition of a native language significantly more challenging. Thus, in biolinguistic context the critical period is uniform and independent of the idiosyncrasies of the language acquired.

Alternatively, in usage-based context the attainment of proficiency in a language is viewed as a learned skill, most successfully achieved in early childhood. Significantly, a notion of “language size” is introduced to stand for limitations in complexity of language system, e.g. in the size of the lexicon, but in the complexity of rules, phonological, semantic, grammatical as they adapt for learnability(Hurford (1991, Hurford and Kirby1999).The language size evolves under the influence of historical, social , cultural factors and is specific to a particular language. Thus, languages are quantifiable and differ in size, which influences the duration of the critical periods.

Importantly, language size evolves in coordination with the critical period, i.e. language change is coordinated with developmental processes. In addition, general maturation and the critical period for language are co-ordinated and both happen in incremental stages, each subsequent stage building on the achievements of the previous one.

“ The key to successful learning ...is the maturational schedule whereby the window of attention (which he calls “ working memory”, emphasis added) gradually expands ...the schedule of expansion is nicely timed to allow just the right amount of time at each stage for the acquisition of enough language, to provide a firm foundation for the next stage of learning “ (Hurford, Kirby, ibid. p. 43.)

And from an evolutionary perspective a continuous process of “self-feeding spiral of language size responding to increase in speed of acquisition and speed of acquisition, in turn, responding to increased language size. “(Hurford, Kirby, ibid. p. 62) would suggest a “ tug of war” between language size and the human brain, likely to have happened during human speciation, a co-evolutionary process which may explain the increase of brain volume in early humans. In sum, language learning and human ontogeny are coordinated and interdependent and human ontogeny has been altered by evolution to facilitate language learning .

6. 2 .2. Language as gradient: challenging the concept of critical period

A challenge to the fundamental assumptions of the generative/biolinguistic perspective in the conceptualization of language, the LF and the critical period is articulated by Balari, Lorenzo(2015). To begin with, the traditional conceptualization of LF as genetically predetermined, i.e. universal and fixed entity, available a priori to language acquisition, and teleologically destined to grow into a predetermined adult state by equally preset stages of development, is replaced with the concept of " *gradient of language*", where the LF is replaced with a flexible combination of a number of bio-cognitive traits, recruited to varying degrees in dynamic negotiation during language development, where initial conditions, i.e. innate predispositions for language may be radically altered by developmental mechanisms, resulting in highly diverse range of adult states of I-languages. The traditional understanding of innate UG as a starting point of language development, is challenged as the musical skills of newborns are featured as the starting point, which allows the child to transform the incoming stream of speech into meaningful segments, i.e. words, and store these in declarative memory, thus compiling " a catalogue of arbitrary pairings of sensory-motor and conceptual percepts" (Balari, Lorenzo, 2015, p.25), as potentially combinable units. In this sense perceptual abilities are used creatively without a priori anticipation for a predestined lexicon. Thus, language here is conceived as emergent in development from perceptual experience and the cognitive ability to identify and store discrete units of meaning and form. This informs the argument for elimination of critical period as a succession of predetermined developmental milestones, and replaces it with a new understanding of development as a fluid succession of developmental states, " following a more or less rigid schedule"(Balari, Lorenzo, 2015, p.27). Thus, a gradient view of language development articulated here conceives of development as a process, where " different components participate to different degrees and intensity at different stages, in which a gradual hybridization is effected"(Balari, Lorenzo ibid, p.33), a process initiated by the formation of discrete phonological categories as a stepping stone for further formation of discrete form-meaning assemblages, i.e. words and morphemes, further supporting grammatical skills.

Importantly, the biolinguistic dichotomy of normal vs. deficient , or impaired linguistic competence, identified as deviation from the preprogrammed developmental schedule, is rendered superfluous , given the gradient nature of competence and variability of developmental outcomes, understood not in terms of absolutes but as a continuum.
Perhaps more importantly, contrary to the currently held dichotomy of innate and learned, nature and culture, here the role of innate and cultural factors in language development is conceived as interpenetration, rendering these " virtually indistinguishable" (Balari, Lorenzo, ibid, p. 28), in this way making the theoretically charted rigid boundaries between the two, irrelevant from developmental perspective.

7. The role of language learners in the evolution of language : Are small children the agents of glossogenesis ?

Scholars diverge in their views on the role of language learners in the evolution of language. The two competing arguments point at :

1.Young children during the critical period. A number of biolinguists, most notably

Bickerton(1984 and elsewhere) explain the emergence of creoles from pidgins during colonization with the natural drive (language instinct) in children to form syntactically complex language as the innate LF is said to inevitably force the formation of a complex linguistic system, despite the extremely impoverished input of the pidgin. The invention by children of Nicaragua Sign Language is treated as an example of the workings of the language instinct in modern times.

2. Young adults. Alternatively, Bybee and Slobin (1982), Slobin,(2004) along with other prominent non-innatists argue that young children are not inventors but more efficient language users. They regularize a chaotic input system but they are not innovators. Young people under 30 years of age are believed to be the likely language creators as it is natural for this age group to look for originality in self-expression. They are also intense communicators. This explains the evolution of language systems as inheritance and innovation, the common denominator in the evolution of languages in different social and cultural circumstances. Thus, very young children are imitators and their role is that of language simplification in preference to regular, easily learnable language forms. Linguistic innovations, i.e. introduction of new constructions and/or novel uses of existing ones are created by young adults in communicative interaction. Thus, the formation of the individual's I-language continues beyond the biological development and includes psychological development of individuality of character.

In short, learners of different ages contribute differently to the evolution of language. Very young children are the agents of regularization and structure formation. Older children, teenagers and young adults are the linguistic innovators, in semantics by introducing new vocabulary items and initiating novel meanings of linguistic constructions and experimenting with new uses of known grammatical forms.

Summary and conclusions

The place of organismal development in evolution has a long and checkered history. It has recently been revived by a relatively new theoretical paradigm in evolutionary biology, the Extended Evolutionary Synthesis(EES) which attributes crucial role of epigenesis in the diversification of organismal morphology and consequently influences the trajectory of evolution by altering genomic expression. Importantly, changes in epigenetic mechanisms are influenced by the environment which exerts selection pressures on biological forms and their behaviours and by this indirectly influences genomic expression.

In human species culture and learning is a major factor in the environment in which human developmental processes take place. And language development guides language evolution. In the study of language evolution human development has become a focus in both dominant perspectives. The biolinguistic understanding of the role of development in the evolution language has changed from initial significant reliance on genomic factors in the phenotypic expression of LF as biological growth of UG, later introducing a more significant role of developmental mechanisms by fixing parameter choices , informed by experience , although limited by genetically predetermined binary alternatives. The Minimalist program envisions a major shift by significantly reducing the influence of innate factors and attributing a major role to learning from experience.

In a usage-based context the evolution of the human body and mind during human speciation and especially the increase of general intelligence, in addition to iterated language learning in different cultural and social contexts over generations of learners is the answer for historical changes in languages and linguistic diversity.

That said, I have argued for integrative approach, i.e. that both biological evolution of developmental routines influenced by language learning, i.e. a process known as the Baldwin effect, by which through co-evolution of language as learned behaviour and various aspects of the human organism, some key aspects of language have become instinct-like predispositions incorporated into a form of language faculty. This incorporation of culture into biology has assured reliable and uniform development of the fundamental aspects of language to nature, demonstrated by early bio-cognitive development in young children, while the idiosyncrasies of language systems continue to be learned and evolve, driven by the creativity of young adults, while subjected to social and cultural influences. In short, language evolution is influenced by the coordination of nature and nurture which interact by integrating biological and psychological development.

The article aims to contribute to deeper understanding of the role of language attainment during ontogenesis by combining and reinterpreting available knowledge from various competing perspectives for a more comprehensive understanding of the evolution of language.

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