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Language follows a distinct mode of extra-genomic evolution

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Abstract

As one of the most specific, yet most diverse of human behaviors, language is shaped by both genomic and extra-genomic evolution. Sharing methods and models between these modes of evolution has significantly advanced our understanding of language and inspired generalized theories of its evolution. Progress is hampered, however, by the fact that the extra-genomic evolution of languages, i.e. linguistic evolution, maps only partially to other forms of evolution. Contrasting it with the biological evolution of eukaryotes and the cultural evolution of technology as the best understood models, we show that linguistic evolution is special by yielding a stationary dynamic rather than stable solutions, and that this dynamic allows the use of language change for social differentiation while maintaining its global adaptiveness. Linguistic evolution furthermore differs from technological evolution by requiring vertical transmission, allowing the reconstruction of phylogenies; and it differs from eukaryotic biological evolution by foregoing a genotype vs phenotype distinction, allowing deliberate and biased change. Recognising these differences will improve our empirical tools and open new avenues for analyzing how linguistic, cultural, and biological evolution interacted with each other when language emerged in the hominin lineage. Importantly, our framework will help to cope with unprecedented scientific and ethical challenges that presently arise from how rapid cultural evolution impacts language, most urgently from interventional clinical tools for language disorders, potential epigenetic effects of technology on language, artificial intelligence and linguistic communicators, and global losses of linguistic diversity and identity. Beyond language, the distinctions made here allow identifying variation in other forms of biological and cultural evolution, developing new perspectives for empirical research.

Introduction

Key concepts of historical linguistics and evolutionary biology share their roots in the tree models that became established in the 19th century [1]: extant similarities are best explained by descent with modification from a shared root. Just like the combination of non-accidental similarity and systematic differentiation between beak shapes among Galapagos finches point to a shared ancestral species, so does the combination of non-accidental similarity and systematic differentiation among words in Indo-European languages (e.g. English *hand*, Nepali *hāt*; English *eight*, Nepali *āṭh*) point to a shared ancestral language. Despite this joint insight, research on biological and linguistic evolution developed independently from each other for more than a century. It is only recently that contact between the two fields was re-established, driven by spectacular successes in estimating language phylogenies and trait histories [2,3]. Independently of this, biologists have increasingly recognized the impact of extra-genomic modes of evolution, launching a highly successful program on cultural transmission [4, 5].

These success stories suggest a far-reaching formal unity of all evolutionary processes. Biological evolution and the various manifestations of cultural evolution all seem to rest on es-

essentially the same principles and therefore afford a generalized theory and a shared toolkit of methods [5, 6]. Yet, this unification continues to be challenged by unresolved debates about how biological evolution interacts with cultural evolution in language [7–11] and by methodological developments that are increasingly responsive to problems that seem specific to biological [12, 13] or linguistic [14, 15] evolution.

These ongoing challenges call for a re-assessment of how the different modes of evolution compare and interact with each other. To be sure, all modes of evolution rely on the same core process: a mechanism producing variation (“mutation”, “change”) and a mechanism transmitting this variation (“inheritance”, “learning”), potentially with reduction (“selection”, “drift”, “bias”) (see Box 1 for a glossary of terms). Beyond this core, profound differences arise. This has been repeatedly noted, mostly by contrasting biological and cultural evolution [5, 16], or biological and linguistic evolution [1, 6]. However, linguistic evolution, i.e. the way in which languages change and diversify, differs in critical ways from other types of cultural

Box 1. Glossary

Absorption: transition into a state (“absorbing state”) that cannot be left.

Adaptiveness (fitness): extent to which a structure is experiencing stabilizing selection in the relevant niche, i.e. the state at which the structure responds to the affordances of the niche sufficiently well for preservation and propagation.

Bias: differences in the probability of a mutation or change in evolution (or the causes or the outcomes of such differences).

Complexity: amount of components linked together in a structure in unpredictable ways.

Drift: reduction of diversity through random sampling.

Epigenetics: environmentally induced alterations of genome activity with phenotypic effects, inherited through the germ line over a few generations and potentially modulating selection pressure and gene mutability (evolvability).

Ergodicity: property of a process where all states or parts of a system can always be reached within finite but randomly varying time.

Evolution: process that generates variation and transmits this variation, possibly in reduced form.

Language: either (i) a system of conventions governing the structure, composition, expression, and interpretation of meaningful signals, used by specific people at a specific time in a specific place, or (ii) the faculty for any such system, as a phenotypic trait of the human species. We refer to (ii) as the **language faculty** (understood in the broad sense [17]).

Macroevolution vs microevolution: processes between (macro) vs within (micro) distinct evolving lineages, i.e., when they no longer evolve as a single unit (for example because organisms cannot interbreed, speakers cannot understand each other or tool parts cannot inter-operate).

Substrate of evolution: the physical environment(s) within which evolutionary processes take place, e.g. nucleotide chemistry, neural systems, ecology.

Mode of evolution: the combination of specific mechanisms of variation, transmission, and selection that is characteristic of an evolving system.

Neutral evolution: transmission with variation but without bias or selection.

Niche: the ecology in which a structure is expressed and exposed to selection.

Plasticity: varying adaptiveness of phenotypes generated by differences in genome activity (for example through epigenetics), thereby modulating selection pressure.

Selection: differential choice of variants for their adaptiveness, limited by the amount of available genotypic variation and constrained by developmental pathways or scaling laws (e.g. Kleiber’s Law or Zipf’s Law).

Stationarity: distribution of state and state transition probabilities towards which ergodic Markov chains converge in infinity.

Transmission: replication of a structure, possibly with errors.

Variation: alteration (mutation) vs preservation of a structure, subject to physical and computational constraints.

evolution. This restrains the utility of two-way comparisons. Here we will show that linguistic evolution has specific characteristics of its own, siding with biological evolution in some and with cultural evolution in other respects. These specific differences are important because they have major methodological consequences and open new avenues for understanding the relationship between biological, cultural, and linguistic processes.

We proceed by developing these differences mainly on the basis of those well-understood instances of evolution that have dominated the discussion. In biology, we focus on eukaryotic evolution of multicellular organisms. In culture, we focus on technological evolution in humans, i.e. the archeologically documented history of artifacts and tools. In language, we focus on the reconstructible history of languages over the past ten thousand years or so. We then take these differences to define a new framework for exploring interactions and transitions between modes of evolution, expanding our purview onto less well-understood instances of evolution, such as the possible co-evolution of language with technology or the evolution of communicative plasticity in early hominins.

Novelty and stability vs ergodicity and stationarity

While all modes of evolution subsist on continuous variation, a hallmark of biological evolution is the notion of **novelty** and **stability** at the level of the phenotype [18]. Biological evolution tends to yield novel forms that fit into specific niches, supported by varying degrees of plasticity and niche (co-)construction, and limited by architectural, phylogenetic, developmental and demographic constraints. Once they sufficiently fit under these conditions, phenotypes are roughly stable. When fitness is reduced, mostly due to environmental change, natural selection favors new phenotypes, often without precedent [12].

The faculty of language is a defining trait of the human phenotype. It evolved once as a novel trait fitting into the specific niche of human communication, sociality, and biology. It is a stable trait: no matter which language we look at, the faculty of language enables open-ended communication, creative cognition, and richly structured cooperation, it can be learned and processed by any human (pathologies aside), and it operates under similar physical and anatomical conditions. There is no evidence for any fundamental change of the faculty, not even when the primary modality changes from spoken to signed [19], or after extreme social disruption [20] and profound cultural transformations, such as the introduction of farming [21]. Innovations in response to niche changes are rare and limited to specific sound patterns. Most notably, changes in tooth use enabled new labiodental sounds (e.g. “f” or “v”) [22, 23], and genetically-influenced changes in pitch processing decreased the use of pitch distinctions for meaning differentiation (known as linguistic tone) in some populations [24, 25]. No other innovations have been reported for the faculty of language in reconstructible history.

At the same time, the language faculty is fundamentally dynamic. Within the state space defined by its niche (Box 2), language is subject to relentless diversification into varieties (dialects, sociolects, etc) and new languages [10, 26]. We refer to this intrinsic dynamics of the language faculty as **linguistic evolution**, as opposed to its biological evolution. Linguistic evolution follows from the social function of language: languages diversify in response to social clustering [27, 28], providing ubiquitous, continuously updated identity markers and creating a sense of belonging [29–34].

These dynamics and their function are a key design feature of language. But how do they square with the biological stability of the language faculty? The answer for this apparent contradiction comes from an intriguing observation that linguists have made since the 19th century (Box 3): the dynamic is full of cyclic developments [47]. A famous case is known as “Jespersen’s cycle”, where negation oscillates between short and long forms: English, for

Box 2. The state space of language. Variation in language is extensive but limited by the communicative (e.g. information-theoretical), social (e.g. trust-building, identificational), neuro-cognitive (e.g. developmental, computational, processual) and physical (e.g. acoustic, anatomical, geographical) niche where it operates. While linguists capture this variation by a wide range of descriptive tools (e.g. variables describing individual constructions, annotations of texts, features in syntax or in phonology, properties and meanings of words, etc.), current databases [35] converge on ever more narrowly defined variables (e.g. differentiating word orders not for entire languages, but conditioned on specific contexts) [36, 37]. The data are mostly discrete, but there is a growing interest in continuous variation, measured for example acoustically [38, 39] or neurobiologically [40, 41]. An unresolved question is the extent to which variables are causally connected with each other, forming evolving systems [36, 42], and it remains equally debated how exactly the various dimensions of the niche delimit the state space of the language faculty — for example whether the state space is mostly defined by communicative and conceptual or by computational and formal principles, or which aspects of the state space, if any, are fixed by learnability constraints [10, 43].

Box 3. Myths about the dynamics of language. Like other everyday phenomena, the dynamics of language are the target of myths and folk theories. Two popular myths in particular hinder evolutionary research:

Myth 1: “Languages become simpler over time.” This myth seems inspired by the observation that Modern English word forms are simpler than those of related ancient languages like Latin or Sanskrit. But counter-examples abound. Maithili, for one, has much more complex verb forms than Old Indo-Aryan, from which it descends [44]. In general, languages usually become more complex because of what is technically known as grammaticalization [45] (where words become grammatical markers, e.g. the literal “she is going” became a future tense marker in “she is going to go”), and simpler because of erosion or regularization, in a cyclic manner (e.g. the future marker is often reduced to “gonna” in colloquial English).

Myth 2: “Languages evolve faster than organisms.” This myth comes from comparing the millions of years it took humans to diverge from other primates with the hundreds of years it took English to diverge from other Germanic languages. But specific aspects of languages and specific aspects of human phenotypes have evolved within similar time depths. For example, words for ‘leg’ in Austronesian [46] (linguistic evolution) and aspects of pitch processing in Europe [25] (arguably genetically based, and thus biological evolution) apparently evolved within the same time span of roughly 10,000 years. The rate or speed of evolution is a property of the individual unit that evolves under a specific condition (with a lower bound set by the unit’s generation time). It is not a property of the overall mode of evolution.

example, started with “ne”, extended it to “na wiht” and similar expressions meaning “not a thing”, then shortened it again to “not” and “n’t”, and now colloquially expands it again by “nothing” in some dialects (as in “she didn’t do nothing”). In modern work, this cyclic dynamic is successfully modeled by (first-order) Markov processes [48–52] that are **ergodic** [48], i.e., all states in a transition chain can be reached in finite but randomly varying time (Figure 1A). This means that there can always be languages in all states (Figure 1B). For example, certain word order patterns have higher probabilities than others because they are easier and preferred, but, given ergodicity, there can always be some languages that use an otherwise dispreferred pattern [53]. A mathematical implication of ergodic processes is that they approach **stationarity** after some time, i.e., the process converges on unique transition probabilities between the states and their associated probability distribution. While the expected time varies greatly, current research suggests that stationarity is often well approached within reconstructible history, at least for grammar [53–57] (cf. *Implications for Methods*).

This property resolves the apparent contradiction between the stability of language in biological evolution and its dynamics in linguistic evolution. What has adapted and stabilized biologically is the total stationary probability distribution at the species level, not the individual languages. For biological evolution it suffices that the language faculty, as a phenotypic trait of the species, has stationary probabilities that are adapted to the niche where it operates.

in the niche of the language faculty, for example how the food we eat affects our teeth and thereby allows a new type of sound, labiodentals. This innovation is not a regular outcome of linguistic evolution. Quite the opposite, the innovation re-defined the niche conditions of linguistic evolution, changing to a state space that now allows Markovian transitions to and from labiodentals, with characteristic stationary probabilities [22]. The lack of radical novelty within linguistic evolution itself invalidates attempts to take patterns in linguistic evolution as potential mirrors of how the language faculty might have emerged in the biological evolution of our species [9, 10, 67–69]. Language change just does not display the directional development that marks the evolution of the language faculty as an entirely novel trait, unique to our species.

Third, linguistic evolution is far more prone to reversals and duplications than biological evolution, which tends to follow Dollo's Principle of Irreversibility. Because of ergodicity a linguistic structure can easily disappear from a language and reappear centuries later, like in the example in Figure 1B [54]. For the same reason languages can develop structures repeatedly [47], sometimes accumulating forms that serve exactly the same function, as has happened for example in redundantly blown-up verb forms in Sino-Tibetan [70]. Given this, evolutionary models based on maximum-parsimony and distance criteria are fundamentally at odds with linguistic evolution. Furthermore, the ergodicity of linguistic evolution implies that processes of the Wright-Fisher type, which include absorbing states, cannot be applied to estimate coalescence times of languages. Such processes are successful in modeling how innovations spread in a speaker population [9, 52, 57, 71–74], i.e. for linguistic micro-evolution. By contrast, linguistic macro-evolution requires models that exclude absorption and fixation. Otherwise, languages would stop changing once they reach an absorbing state. This conflicts with the function that language change has in social differentiation.

In all these respects, linguistic evolution is different not only from biological but also from many forms of cultural evolution. Technological evolution in particular is characterized by the same alternation between stable solutions and radical, discovery-driven innovations in specific utility niches that characterizes biological evolution. Just as technologies remain stable (e.g. metal knives) until they are replaced by new ones (e.g. laser cutters) serving new purposes (high-precision edging), so too organisms generally remain stable until they undergo directional changes as selective response to changes in the environment. Technological and biological evolution are not constrained by ergodicity. Instead, they are characterized by competition in adaptiveness, and tend toward ever-growing and cumulative ("ratcheting") complexity [75] (Figure 1C).

Does the difference between stationarity and stability mean that the outcomes of linguistic evolution are different from biological and cultural evolution in all respects? Not quite. Stationary probabilities are independent of absolute transition rates [76]: Like in biological and cultural evolution, languages evolve at an uneven pace, sometimes faster, sometimes slower (Box 3). In language, the processes generating variation, and thus the rate of change and evolvability, are social ones, reflecting ideologies about language change, social network sizes and densities, the amount of second language learners or the need for, and effects of, group distinction [29, 30, 32–34, 77–79]. For example, deliberate exaggeration of differences after language splits ("schismogenesis") often speeds up evolution, similar in effect to bursts through adaptive radiation in biological evolution [46, 80].

Obligate vs optional verticality

Like genes, languages must be passed on from generation to generation to evolve. When vertical transmission stops, languages and species go extinct, currently at an alarming rate in both cases [81].

This basic observation notwithstanding, it has often been cautioned (at least since Kroeber's 1923 anthropology textbook) that linguistic evolution might be affected by critically more horizontal transmission than (eukaryotic) biological evolution [82]. Words and structures spread from language to language by various copying and transfer processes [14, 62, 83]. For example, many languages of Europe share similarities not because of common descent but because of repeated copying over the centuries [84].

The reason for this apparent contradiction is that linguistic evolution relies on two distinct transmission processes of social learning [72, 73, 85–88]: First, alterations based on choice, copy, or error spread (horizontally) among adolescent and adult speakers, shifting and diversifying the probability distributions of words and structures. Second, if this statistical signal is strong enough, the alterations are acquired (vertically) by the next generation of children. Both processes are required for language change. Acquisition alone is insufficient. Children are highly resilient and conservative learners, approximating, not changing, the input they receive. But spread alone is also insufficient. Not every slang expression, loanword, or other alteration makes it into the next generation. Evolution only happens when an alteration is acquired by the next generation. This is comparable to the social spread of gene expression in epigenetics: to have an effect on evolution, it must make it into the germline.

This **obligate verticality** explains the original 19th century observation that both languages and organisms diversify by stepwise modification from a common root, with true homology or “cognacy”, as it is known in linguistics. Obligate verticality guarantees the regular, step-by-step modification that is necessary to establish this. For example, the cognacy of German *Zahn* ‘tooth’ with Latin *dens* and Nepali *dãt* is established by stepwise and regular modification of *d* into *t*, as still attested in English *tooth*, and then of *t* into *z* (pronounced *ts*). Deviations from regularity give away loanwords. English *dentist*, for example, was borrowed, and is not a direct cognate, because *d* regularly changed to *t* in English (and it was borrowed after this sound change happened).

It is this regularity in word forms that allows detection of common descent and therefore inference of trees of the kind shown in Figure 1B [3, 89]. The trees define vertical lineages through generations, channelling the transmission of any kind of structure, beyond cognates. Once adopted, loanwords and copies (e.g. perfect tenses with “have” in Europe) also follow the same vertical channel as cognates, blending in with native words and structures [84, 90]. Again, the vertical channel is essential; copying alone would have no evolutionary consequences. This obligate verticality makes it possible to statistically separate spread events from the vertical tree structures [14, 46, 90–93], much like in biology [94–96].

Nonlinguistic cultural evolution is fundamentally different in these regards. Cultural traits evolve by copying horizontally and obliquely, such as in the spread of farming or cutting technologies (Figure 1C), or even through systematically skipping one generation, such as the transmission of specific ritual practices in parts of indigenous Australia [97]. Technology can die out and be re-discovered after long gaps, such as cement-based concrete [98]. None of these processes critically necessitates a vertical process akin to the germline in biology or the acquisition process in language. Unlike in language, the transmission of technology does not hinge on feeding (noisy) statistical input to children who have matching neuro-cognitive learning skills [99]. Instead, it requires a variety of teaching, copying, and trial-and-error procedures [100] that are usually free of critical period constraints in infants .

As a result, cultural evolution is typically less gradual and less incremental than linguistic or biological evolution [4, 5]. The evolution of cutting technology, for example, is full of abrupt breaks and parallel developments when new possibilities are discovered and new tools developed (Figure 1C). The lack of homology/cognacy in cultural data furthermore means that its evolution is typically better captured by directed networks than trees, and research focus-

es more on micro-evolutionary diffusion than on macro-evolutionary diversification [101]. In some cases, however, a linguistically inferred tree can be taken as a proxy of social differentiation and then the macro-evolution of technology or other cultural traits can be successfully modeled [101, 102]; and sometimes there are enough historical data to trace tree-like evolution longitudinally [103, 104].

Two substrates vs. one substrate

A key property of biological evolution is that selection operates in a different physical substrate than the generation and inheritance of variation: selection operates through the interaction of phenotypes — as gene “vehicles”[105] or “interactants”[106] — with their ecology; variation and inheritance operate through processes in nucleotide chemistry, the genotype. Both processes are usually involved in creating stability, while the genotype alone typically rests on stationary processes of nucleotide substitution at each site (often adaptively neutral), comparable to the stationary processes of linguistic evolution. But in linguistic evolution there is only one substrate for the operations; there is no genotype vs phenotype distinction [87], and selection operates in the very same physical substrate as variation generation and inheritance, viz. in the social learning processes enabled when utterances are communicated and processed by interlocutors’ brains [87]. This is similar in cultural evolution, which also foregoes the genotype vs. phenotype distinction and relies on a single substrate for variation generation, inheritance, and selection in the form of interaction between individuals. Two consequences follow.

First, because variation is generated in the same substrate in which selection operates, the forces that shape selection, such as processing and learning preferences, or cultural utility, can also directly bias probabilities of change. Indeed, some changes in language [6, 57, 107, 108] and culture [109] are intrinsically more likely than others, yielding results similar to those of selection among random replication errors. Disentangling these two options — sometimes called ‘source-oriented’ (or ‘mutational’) vs. ‘result-oriented’ (or ‘selectional’) evolution in language [110] — is challenging but increasingly possible by contrasting source-conditioned entry rates with the overall exit rates of a given state [111]. The issues do not arise as much in biology because biased mutations, although important, are limited to the genotype level [112]. It is only through epigenetics that genomic expression can be environmentally biased and thereby operate in a similar fashion as natural selection [113].

Second, since linguistic and cultural evolution operate in a single substrate that relies on the interaction between individuals, they are necessarily open to deliberate intervention in the form of conformity needs (for example strategically adopting new words, or new tools and rituals) or strategic tinkering (for example through language policies or in engineering), unlike biological evolution (which can be tampered with only by cultural innovations like selective breeding and genetic engineering). In practice, however, the amount of active intervention is limited in linguistic evolution. Indeed, many properties of language (for example verb inflection as in *eat* vs *eats* vs *ate*) tend to resist conscious choice [32, 46]. They are instead determined by the total success in processing, learning, and communication over thousands of daily utterances [22, 36, 57, 114] (avoiding for example too many irregularities of the *eat/ate* type).

Implications for methods

Our comparisons suggest that, despite a common core in mechanisms of variation, transmission and selection, linguistic evolution has a dynamic distinct from other modes of evolution. It differs from the others in the ergodicity and stationary nature of its states. It sides with

biological evolution in the necessity of vertical transmission, but with cultural evolution by foregoing a genotype vs. phenotype distinction (Figure 2).

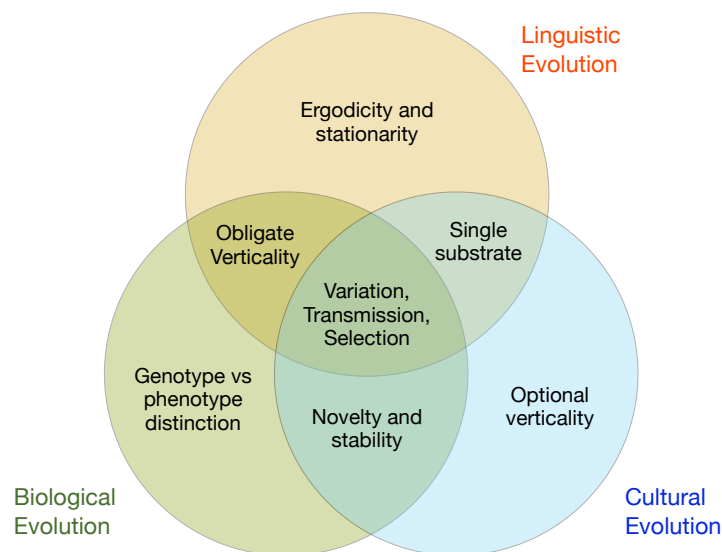


Figure 2: Linguistic, biological, and cultural (in particular, technological) evolution share a common core but each mode of evolution also has a property that distinguishes it from the other two: the ergodicity and stationarity of linguistic evolution in contrast to the alternation between stability and novelty in biological and cultural evolution; the genotype vs phenotype distinction of biological evolution in contrast to a single substrate for variation, transmission, and selection in linguistic and cultural evolution; and the optionality of vertical transmission in cultural evolution in contrast to the obligate transmission from one generation to the next in linguistic and biological evolution.

This profile has several methodological consequences. We have noted in our discussion (i) that at the species level language is best described by stationary probabilities, and not, as traditionally done, by “universals” that are qualitatively derived by abstraction over, or generalization across, individual languages, (ii) that regular patterns in linguistic evolution cannot recapitulate the biological evolution of the language faculty, (iii) that linguistic evolution supports true homology and therefore tree construction, unlike cultural, but like biological evolution, and (iv) that in linguistic and cultural evolution we can (and should) tease apart source-oriented (mutation-biasing) and result-oriented (selection-driven) effects.

But the profile also highlights the most important methodological challenge that remains for linguistic evolution: how to estimate stationary probabilities at the species level. Much progress has been made, especially because, unlike in biological evolution [12, 115], available likelihood methods for Markov chain models are not challenged by absolute novelty, and because these methods have almost completely superseded parsimony and distance methods that are (as noted earlier) at odds with ergodic processes. But there are also many open issues that remain.

For one, despite their wide-ranging success, we do not know whether current Markov chain models are sufficient in all areas of linguistic evolution. One open question is whether and how ergodicity and stationarity in linguistic evolution can also be captured for continuous traits (cf. Box 2), for example by adding bounds [116] or constraining forces [117, 118] to basic Brownian motion processes. This has been explored only very rarely [119, 120], and it is unknown how well these models correspond to language change at the microevolutionary level.

Another challenge comes from language’s state space. The state space of word forms is large, as there are, for example, many ways of naming things. This considerably increases

the time to visit, let alone re-visit, each state. The upside of this is that word forms preserve signals of cognacy over longer time than any other property of language, allowing reconstruction of language trees (cf. *Obligate vs Optional Verticality*) and occasional approximations of individual word form evolution with non-ergodic models [51]. After about 10,000 years, however, states start to re-appear in the form of look-alikes [3, 89], word forms that resemble each other by mere chance or because of recurrent sound-meaning associations [121, 122] and word formation patterns [123]. This explains why older language families are exceedingly difficult to demonstrate and why attempts to estimate a world tree of languages meet skepticism among linguists.

The downside of the large state space in word forms is that it is difficult to assess whether estimates of stationary probabilities only characterize the current sample or whether they allow inferences to human language as a whole. Structural traits in grammar and phonology usually have smaller state spaces, but when they are causally connected with each other (cf. Box 2), the time to reach stationarity increases there as well, possibly beyond known linguistic history [48].

The issue is compounded by the fact that in the absence of linguistic data older than ca. 5,000 years (from which we have the earliest writings), models need to co-estimate the impact of population history on language distributions (as well as the uncertainty about this impact). Extant linguistic distributions are heavily skewed by geographical conditions [124–126] and the vagaries of population history [48, 77, 78, 90, 93, 127], such as the agriculturally induced spreads of large families like Indo-European and Sino-Tibetan [128]. Partly as a result of these spreads, nearly half of the known language families are attested only by a single, isolate member [90]. There are only few proposals for how to estimate the evolution of such degenerate families together with that of language families with more informative phylogenies [53, 90].

On the other hand, more and more studies identify causal mechanisms under which stationarity is expected, with specific asymmetries. Various experimental techniques and analyses of naturally produced language data have revealed, for example, that during linguistic evolution, compositional expression is preferred over holistic expression [129, 130], recursive over one-off hierarchy [54], shorter over longer dependencies [120, 131], simpler agent than patient coding [132, 133], anterior over posterior voicing contrasts [134], and semantically more over less coherent categories [135–137]. These lead us to expect asymmetries in stationary probabilities --- sometimes called “diachronic biases” [36] --- that shape the intrinsic dynamic in the language faculty. Some of the asymmetries are grounded in biology, as manifest in independently traceable processing and learning preferences (for example favoring agents and coherent categories), while others derive from the general laws of information theory (for example expression/compression trade-offs) or (bio)physics (for example the acoustics of consonants) [26, 36].

We suspect such asymmetries to be similar for all human populations because they hold at the species level, and, allowing for some amount of random variation, this has been confirmed in recent studies that test the idea explicitly [53, 132]. When they differ among populations, this points to potential variation in the niche of the language faculty, and we will review possible cases below. Importantly, however, since asymmetries bear only on the stationary probabilities of a state, and do not introduce novel states into the language faculty, variation in asymmetries remains firmly within the ergodicity of linguistic evolution. This explains why such variation does not hinder any human infant from learning any language. When a language runs counter to global preference it incurs slight disadvantages in one or the other aspect of learning or processing, but it can still be learned. Brains are plastic enough to cope with any choice in the ergodic space of the language faculty.

Implications for interaction and co-evolution

If linguistic evolution differs from both biological and cultural evolution, how do these modes of evolution interact with each other? Could they co-evolve? Specifically, how does linguistic evolution interact with the biological evolution of the language faculty, and how does it interact with cultural evolution? Can language evolution interact with cultural evolution, for example in technology? These questions are difficult to ask, let alone answer, without the distinctions we propose. As we suggest below, many of these potential interactions open exciting avenues for research (Figure 3).

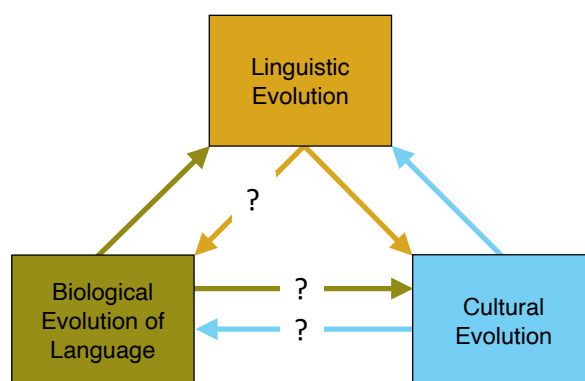


Figure 3. Interactions of the three modes of evolution proposed. Much is understood conceptually, though less so empirically, about how biology constrains linguistic evolution and how linguistic evolution interacts with cultural evolution (plain arrows). The other three links (arrows with ‘?’) raise new questions, opening avenues for future research.

Linguistic evolution and biological evolution

Linguistic evolution is the product of biological evolution. The biological evolution of the language faculty has not only defined the common state space within which all languages serve their communicative and cognitive functions, but it has also produced the ergodic dynamics that makes language a tool for social distinction. It is unknown why and when this combination of functions evolved. The combination is evolutionarily expensive because it requires intensive learning and regular coping with neurocognitively and communicatively dispreferred states. Progress here will depend on a deeper understanding of how social structures evolved in the hominin lineage. One intriguing hypothesis is that these aspects of linguistic evolution emerged when societies of mutual trust and mating grew beyond the point where one could know all members individually [33, 138]. The idea is that linguistic evolution creates identity tags for these societies that are continuously available and hard to imitate for adult outsiders [34], perhaps extending earlier uses of vocalizations as group signatures [139]. As a result, language has become a privileged instrument in schismogenesis (although of course not the sole instrument that humans use).

Biological evolution is also likely to have defined specific asymmetries in stationary probabilities. To pick up some of the findings mentioned above, the preference for compositional and recursive expression in linguistic evolution rests on the neurobiological evolution of signal segmentation and recombination abilities [7, 140, 141], which have likely been selected for their communicative, acquisitional, and computational efficiency [9, 10, 142]. Similarly, the preference for simpler agent than patient expressions in linguistic evolution probably derives from a deeply rooted preference for agents in primate event cognition [133].

Can there be reverse effects? Can linguistic evolution impact the biological evolution of the language faculty? At first sight this is plausible in analogy to how cultural evolution impacts biological evolution in domains other than language [143], as when for example the invention of dairy farming has forced genetic adaptation in the form of developmental persistence of lactase, or the invention of sunscreen and vitamin D supplements masks genetic drivers of skin cancer and calcium absorption, respectively [144]. However, for such effects to impact genomes, cultural patterns must stabilize in a population for long enough periods. This is different in linguistic evolution, where traits never stabilize: their ergodicity means that they always remain “moving targets” [10] (Figure 1B). While this does not necessarily exclude any language-gene coevolution (as it could be rapid in principle, see Box 3), no case has been demonstrated with biological evidence, despite two decades of intensive search and suggestive computer simulations [9, 11, 69]. The relationship between sign language and monogenic deafness is sometimes cited as an example [145]. However, the evidence for coevolution remains controversial because spontaneously rather than institutionally established sign language communities show much less assortative mating than is needed for an impact of language on genes [146, 147]. The drift towards sign language is therefore more likely a special case of linguistic evolution with a change of sensory-motor support that has emerged in populations with prevalent deafness.

An alternative but unexplored possibility is that epigenetics might be at play in linguistic evolution, like in other aspects of how humans interact with their social environment. Epigenetic effects operate within an individual’s lifespan and are therefore exempt from the moving target problem. Epigenetics works by adding chemical tags to DNA strands, which then switch gene expression on or off, while the DNA sequence remains unchanged. To be inherited, however, the tagging has to be present in the germline, with sufficient presence in the gametes, and escape cleaning processes. A particularly promising avenue to address language-gene interactions at this level are genes expressed in brain regions that have most recently evolved, such as Broca’s area [148], or genes expressed in computations that are key for language, such as neural oscillations for parsing, chunking and planning speech [149–155]. If such epigenetic tags make it to the next generation, they could potentially also alter the biological evolution of the language faculty.

A further possibility is that linguistic diversification leads to gene flow barriers, thereby structuring genetic populations. While current samples indeed reveal many cases of parallel genetic and linguistic diversification [156], the effects of this are expected to be adaptively neutral. To date, we are not aware of any mechanism that would make allele frequencies depend on the distribution of specific linguistic structures or words.

Linguistic evolution and cultural evolution

The cultural evolution of subsistence types [125], social complexity [157], and language attitudes [30] is likely to have impacted diversification rates in linguistic evolution, although effects are often difficult to distinguish from co-varying factors of demography and ecology [77, 78, 124, 126] that might have been at play in the biological evolution of the language faculty as well (e.g. driving the use of language for social identity).

Cultural evolution has also impacted the stationary probabilities of specific language states. The most pervasive effect is in the lexicon where cultural innovations put pressure on speakers’ application of linguistic operations like metaphor [158, 159] to label new artifacts and structures (e.g. using a word for “circle” for the newly invented wheel, or a word for “web” for the newly invented internet). Effects outside the lexicon include for example how changes in language attitude might have impacted the stationary probability of grammatical

complexity [30], along with demographic admixture of second-language speakers who tend to lower specific aspects of this complexity [160–162].

A more controversial case is the potential impact of literacy on linguistic evolution. While literacy is known to impact spoken language processing [163–165], and often favors more complex expression styles (written legal document vs. everyday conversations), there is no evidence to date that it impacts linguistic evolution. An in-depth case study found only indirect and marginal effects [166], but large-scale models are lacking. At present, the evolution of autocompletion technologies and machine translation seems to impact preferences for certain formulations and word choices over others [167, 168], but the long-term consequences of this are unknown.

Effects from linguistic on cultural evolution are less well studied, chiefly because they demand complex co-evolutionary models where changes in language reinforce changes in cultural practices and vice-versa, with potential time lags. There are many intriguing observations and open questions — for example on the relationships between kinship terminology and social interdependence norms [169], or between spatial reference and architectural or ritual norms [170] — but co-evolutionary modeling at a global scale is lacking. Another promising area for research on language-culture co-evolution is how the application of specific metaphors might have impacted discoveries in science and developments in technology, for example how the “tree” metaphor has shaped evolutionary theories and phylogenetic estimation techniques.

Biological evolution and cultural evolution

The language faculty is often claimed to have co-evolved with advanced stone tool technology [171–173], although the underlying neurobiological mechanisms and evolutionary processes continue to be debated [174–176]. Ongoing technological evolution at present poses similar but more pressing questions. We see at least two ways in which current technology might reshape the niche within which language operates and thereby potentially impact the biological evolution of the language faculty.

First, technological evolution has reached a point where we can engineer the brain, and directly act on the brain’s language system. The need to intervene on the brain’s language system primarily arises from the desire to correct disorders that are either acutely acquired (for example post-stroke aphasia) or neurodevelopmental (dyslexia, autism, stuttering, dysphasia, specific language impairment, etc.). Gene therapy of the inner ear is soon to become available as a therapy for monogenic congenital deafness [177, 178]. Neurostimulation already enables functional alleviation of neurodevelopmental, highly polygenic language disorders [179]. The globalization of such direct interventions, gene therapy in particular, will in the long run remove selection against genes that limit engagement with the dominant modality of language, speech.

Second, technological evolution is increasingly delivering efficient brain-computer interfaces, even cortico-computer interfaces [180], allowing for direct decoding of unspoken language from neural activity. To date, most attempts have opted for decoding motor plans [181], a strategy that could in the best-case scenario work as fast as real speech production, though currently working at much slower rates. However, by moving beyond motor plans [40, 182], it might become possible to decode more abstract forms of language, eventually allowing us to bypass the linearization bottleneck and leading to faster and different forms of communication and thinking. If talking mentally to one’s computer via for example EEG became standard, the audio-phonatory loop, which has been a major condition of the language faculty, would be replaced by a loop where the feedback is freed from (bio-)mechanical constraints. In other domains (e.g. sense of agency) such a lack of feedback is known to provoke delu-

sions and schizophrenic symptoms as the brain cannot suppress self-generated neural signals [183]. It is entirely unclear what risks such developments incur and to what extent they might change fundamental operations in language.

Implications for transitions, or the “evolution of evolution”

Another set of questions elicited by our distinctions concerns possible transitions between, and mixtures of, different modes of evolution. Figure 4 charts two transitions that play a central role in language. The red arrow sketches the likely transition from primate to linguistic communication. It started from a communicative and cognitive system that was chiefly subject to biological evolution, changing mainly between species, in response to varied communicative niches. It ended with the within-species dynamic of language’s ergodicity that no longer relies on a genotype-phenotype interaction to evolve.

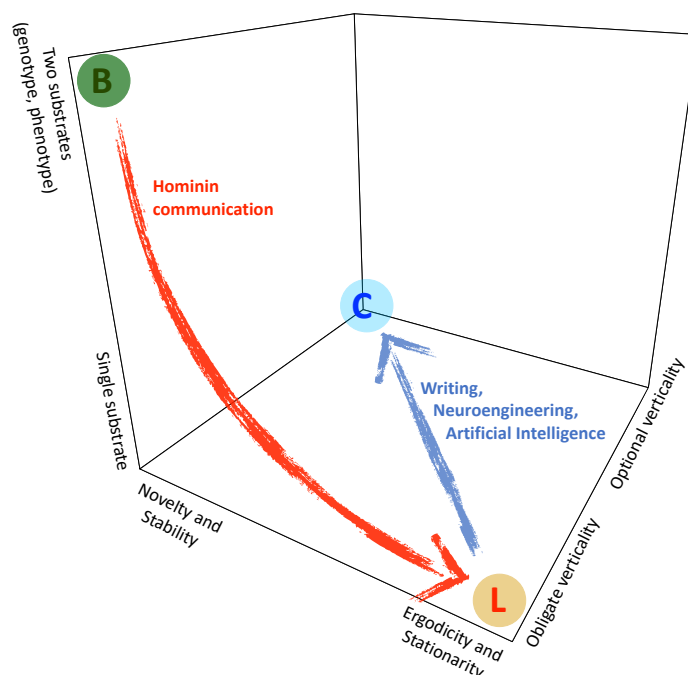


Figure 4. Two transitions between modes of evolution. B = biological (eukaryotic) evolution; C: cultural (technological) evolution; L: linguistic evolution.

The transition is ill-understood but, like so often in evolution, it is likely to have started with a gradual increase in phenotypic plasticity. This relaxed selection pressure, most likely at different rates for different aspects of prelinguistic communication and cognition, e.g. earlier for syntax than phonology [141]. Over time, diversification in vocal behavior was no longer tied to biological evolution, similar to the effects of domestication [184]. In addition, this more diverse behavior has fundamentally re-structured the niche of communication, triggering still increasing plasticity and neural de-differentiation in learning and processing. It is likely that these developments in turn spiraled up diversification until the process outpaced biologically driven evolution. At this point, the system hit the bounds of the ergodic state space that defines our language faculty (Box 2) [10], again quite possibly at different times for different aspects of language.

At the functional level, one candidate mechanism favoring the transition is the use of communicative signals for social tagging, possibly triggered by growing population size (as noted earlier) and enhanced by epigenetic effects from this tagging. An alternative mechanism is

variation as a result of population splits in changing ecologies while inter-breeding and exchange continued among them, a dynamic that has characterized human history early on [185–187].

The transition was likely a lengthy process. Given what can be inferred about Neanderthal behavior [188] and hominin brain evolution [148, 176], it probably started in the early Paleolithic, at least for some aspects of language. It ended only recently, with the emergence of labiodental sounds as arguably the latest addition to the state space.

The blue arrow sketches other key transitions of language, the transitions into culturally evolving technologies. We have already surveyed the impact of neurological engineering and brain-computer interfaces that might change language and its future evolution in fundamental ways. Another example is the use and transmission of language by artificial systems, for example by the various versions of generative pretrained transformer models (GPT) that produce and consume language at rapidly increasing scale.

The earliest transition of language into evolving technology came with writing. Driven by cultural rather than linguistic evolution, writing is not bound to vertical inheritance. It can spread in any direction and with temporal gaps, as when we can now re-learn ancient cuneiform by imitating inscriptions. As a result, writing allows communication across arbitrary distances, to millions of people worldwide and simultaneously, and without identifying ourselves as the source. Furthermore, we can read 2,000 year-old texts, and this makes it possible to borrow long-extinct earlier words (for example so-called Latinisms in Romance, or Tatsama words in Indic languages); it even allowed the re-introduction of a language back into linguistic evolution, as in the rare case of Hebrew.

As a technology, writing also differs from linguistic evolution in that it is not ergodic. It is instead driven by waves of radical novelty, both in forms (alphabets, syllabaries, logographies, emojis, memes etc) and techniques (etching, hand-writing, typing, speech-to-text conversion, etc). One of the most impactful innovations was arguably the introduction of formulas and visualizations (e.g. the number line) when writing down mathematics in the 17th century [189]. Strong impact can also be expected in the domain of emotions, where the ongoing evolution of emojis and video-clip memes changes the way we communicate experiences.

Many more transitions could be drawn in Figure 4 outside the domain of language. For example, the transition from prokaryotic to eukaryotic evolution was characterized by the addition of the germline and the reduction of horizontal gene transfer. These were radically novel structures that enabled rapid increases in complexity.

Some transition lines are arguably more complex. For example, we suspect that the evolution of music and fashion is best modeled as an alternation between innovation-driven technological evolution and ergodic cycles. New instruments (e.g. electric guitars) and fabric (e.g. polyester) allow new styles, but these then seem to be recycled in a stationary process until they are in turn superseded by new instruments and fabrics. More research is now needed to explore how modes of evolution play together in these and other areas of culture.

Conclusions

Our analysis reveals three dimensions in which modes of evolution differ from each other: whether evolution is ergodic or novelty-driven, whether or not it requires vertical transmission, and whether it rests on one or two physical substrates. Each of these dimensions greatly affects the kinds of evolutionary outcomes one can expect as well as the choice of methods to model them. We have developed the three dimensions on the basis of relatively well-understood types of biological, linguistic and cultural evolution. But as noted in the discussion of interactions (Figure 3) and transitions (Figure 4), the three dimensions lead to a

richer space of possibilities. We propose that this framework allows more precise discussions about how various evolutionary processes come about and affect each other. In the long run, we expect broad dichotomies like “cultural” or “biological” to lose importance and to yield to sharper notions. What remains as a unifying principle is the core of evolution: the combination of specific mechanisms for variation generation, transmission and selection.

The distinct mode of evolution that characterizes language opens perspectives that have been off limits for traditional (qualitative) linguistics, i.e. the stationary probabilities of states, with their intriguing asymmetries. This finding in turn expands the question of the biological evolution of the language faculty from its possible states to their characteristic dynamics. These dynamics shed new light on biological evolution, separating for example the effects of inherited traits (like agency detection) from derived traits (like social differentiation) on specific properties of language (default syntax and change dynamics, respectively) when it emerged during hominin history.

Furthermore, carving out the specific properties of linguistic evolution allows us to more sharply examine how language interacts with, and transitions from and into, other modes of evolution, not only with regard to biological evolution, but also with regard to cultural, in particular technological, evolution. This will be especially important in the near future, as we are witnessing rapid developments in technology, in particular genetic and neurological engineering, artificial intelligence, brain-computer interfaces, and social media, which may yield entirely new modes of evolution, involving novel social entities (brain-to-brain, brain-to-machine, crowd-to-crowd) that overrule those that were hitherto built via language. At the same time, ever-faster globalization reduces linguistic diversity at an unprecedented pace. This disrupts the traditional function that language distinctions have as markers of trust and cooperation networks, but the impact of these developments on human society is barely understood.

All these developments come with enormous ethical and societal challenges. It is urgent to recognize and examine them in depth. The analytical framework we proposed here may facilitate this endeavor.

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