

Review

Rethinking foundations of language from a multidisciplinary perspective ☆

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Abstract

The issue of language foundations has been of great controversy ever since it was first raised in Lenneberg's (1967) monograph *Biological Foundations of Language*. Based on a survey of recent findings relevant to the study of language acquisition and evolution, we propose that: (i) the biological predispositions for language are largely domain-general, not necessarily language-specific or human-unique; (ii) the socio-cultural environment of language serves as another important foundation of language, which helps shape language components, induce and drive language shift; and (iii) language must have coevolved with the cognitive mechanisms associated with it through intertwined biological and cultural evolution. In addition to theoretical issues, this paper also evaluates the primary approaches recently joining the endeavor of studying language foundations and evolution, including human experiments and computer simulations. Most of the evidence surveyed in this paper comes from a variety of disciplines, and methodology therein complements each other to form a global picture of language foundations. These reflect the complexity of the issue of language foundations and the necessity of taking a multidisciplinary perspective to address it.

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“(If we see language evolution in a mosaic fashion, as the emergence of an ‘interface’ that integrates a host of largely pre-existing capabilities, then we should not expect to discover any autonomous organs with language neatly packaged.” – William S-Y. Wang (1982; p. 26)

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1. Introduction

The year 2017 marks the 50th anniversary of the publication of *Biological Foundations of Language* [1]. In this seminal work, Lenneberg reinstated the concept of a biological basis of language capacities, and proposed a series of hypotheses on the biological foundations of human language (hereafter, language) that were subject to empirical tests. The abundant evidence in the monograph has been accumulated throughout Lenneberg's academic career. Throughout the eight chapters of the monograph, he delivered a nativism position that children must come with a set of biological predispositions to acquire and use any language (e.g., "Language, as any other type of behavior, is seen as a manifestation of intricate physiological processes" [1, p. 119], or "there are many reasons to believe that the process by which the realized, outer structure of a natural language comes about is deeply-rooted, species-specific, innate properties of man's biological nature" [1, p. 394]). The issue of language foundations raised in the monograph has remained puzzling to researchers of language from various disciplines, especially evolutionary linguistics [2,3], which aims to identify when, where, and how language originates, changes and disappears [4].

The past 50 years have witnessed numerous breakthroughs in evolutionary linguistics as well as other relevant disciplines. The latest technology or methodology and accumulated evidence obtained accordingly have induced many refutations towards the nativism position about language and shed new light on the issue of language foundations. For example, it has been repetitively discovered that many biological predispositions in humans are not specific for language acquisition, but manifest in several non-linguistic tasks, and that many presumably human-unique cognitive capacities are also evident in non-human species. In addition, recently-adopted approaches such as laboratory experiments and computer simulations have quantitatively illustrated the importance of socio-cultural transmissions in shaping components of language, laying out necessary constraints on language processing and acquisition, and driving continuous and dynamic shift of language. All these indicate that our vision of the foundations of language should not be limited to biology and individual learning.

The present article aims to reexamine the issue of language foundations primarily from three aspects: the nature of biological foundations of language, the indispensability of socio-cultural environment of language, and the relations between biological and cultural evolution regarding language. We evaluate selective theoretical and empirical studies after Lenneberg's work. Most of the novel evidence reviewed here results from collaborative efforts between linguistics and a variety of disciplines, including those that Lenneberg paid close attention to in his book (e.g., psychology, anthropology, genetics, and animal behavior studies) and those that have recently been adopted to provide interpretive and quantitative evidence of language acquisition and evolution, such as experimental semiotics, computer simulation, cognitive neuroscience, and others. There is a long tradition of sociolinguistic research investigating actual language use through empirical observational studies, which has also amassed a large amount of evidence on how a speaker's socio-cultural environment in a given speech community influences how he/she acquires and uses language. However, our review tends to focus more on studies using recently adopted approaches to investigate the roles of socio-cultural factors in language evolution.

The rich but non-exhaustive evidence reveals that: the biological capacities relevant for language learning and use could be domain-general and shared by many species, though with different degrees, and therefore, the strong nativism about the existence of language-specific and human-unique capacities for learning and using language becomes groundless; language resulted from intertwined biological and cultural evolution, with no clear watershed between the two throughout the whole evolutionary process, and therefore, in addition to the biological foundations, socio-cultural environment of language is another imperative foundation of language.

2. Many biological predispositions are not language-specific nor human-unique

Lenneberg focused on the morphological and physiological correlates of language in his monograph. He discussed in detail two primary determiners for the sound-making capacities in humans: the shape of vocal tract and the patterning of motor coordination. These properties enable humans, but not other animals, to generate articulate speech. Many discussions in this regard are based on empirical findings in comparative anatomy. This line of research aims to obtain the evidence of presence or absence of critical conformations associated with unique human behaviors like speech, and assumes that unique behaviors like language must be determined by unique anatomical or physiological arrangements [5].

However, the relationship between anatomical structures and cognitive functions is not always straightforward, in the sense that possession of a physiological apparatus does not necessarily imply possession of relevant cognitive capacities. A typical case to illustrate such mismatch between anatomy and capacity is the descent of the larynx in humans, compared to other apes. In line with Lenneberg's thought, Lieberman proposes that the descent of the larynx in humans leads to flexible shapes of vocal tract, thus enabling speech in humans. A lowered larynx, anatomically speaking, creates a two-chamber supraglottal vocal tract consisting of pharynx and mouth. Both chambers can be narrowed or broadened complementarily. During vowel production, a vibrating air column can pass through either first a narrow tube and later a wider one (producing an /a/ vowel), or first a wide tube and later a narrower one (producing an /i/ vowel). This flexibility of the upper vocal tract enables a number of distinct vowel qualities. By contrast, the relatively higher positions of the larynx in non-human apes restrict their abilities of vocal imitation, thus depriving those species of the biological foundation to develop language [6–9].

Lieberman's view has been challenged in both anatomical and functional aspects. First, many factors determining the position of the larynx have little or nothing to do with speech. For instance, human boys on average have a much bigger change in laryngeal position than girls during puberty, probably to mark sexual dimorphism [10]. The evolutionary descent of the larynx in humans may be due more to physiological factors relating to bipedalism, facial reduction, and brain expansion, than to the need of speech [11]. Second, before their larynxes reach the adult position, children can lower their larynxes to produce sounds associated with human speech [12]. Other mammals can also dynamically lower their larynxes during vocalization, probably to generate lower pitch sounds, and thus deliver an impression of a larger body size to deter potential predators in the environment [13]. However, none of these species developed a speech-like vocalization system. This indicates that the presence of a structure might originally serve other purposes or be determined by non-linguistic factors.

In addition to the anatomical structure such as the descent of the larynx, innervation and adequate motor control from the brain are also needed for speech [13]. Anthropological evidence has revealed that the descent of the larynx started as old as *Homo erectus* [14]. Neanderthals had identical hyoid bones to modern humans [15], and their vocal tract lengths fall in a similar range as that of modern human females [6]. Recent evidence in linguistics, archaeology, genetics, and paleontology suggests that Neanderthals might share with us something like modern speech and language [16], indicating that vocal communication might have started to be enhanced by that point. Increase in brain size has also been reckoned before *Homo sapiens*, though probably associated originally with the increase in group size and social complexity [17]. Compared to the descent of the larynx, brain expansion in members of the *Homo* genus appears to be more related to vocal communications, speech, and language.

Chomsky, who provided an appendix to Lenneberg's monograph about the formal nature of language, has extended Lenneberg's nativism position. His theory stresses that humans possess a set of species-specific and language-unique capacities, namely the faculty of language (FL) [18,19], which allows humans to master and use any natural language. Focusing more on syntax than speech, Chomsky proposes a syntactocentric architecture of language [20]. This structuralist view localizes the generative capacity of language in syntax, and states that combinatorial properties of sound and meaning come from syntactic derivations. In addition, Chomsky proposes the existence of a genetically transmitted syntax module in the human brain, which instantiates a universal grammar (UG) [21,22]. UG is intended to specify either the universal properties shared by languages or the developmental constraints allowing children to acquire language. Language acquisition is viewed as a process whereby the principles and parameters coded in UG yield the grammar of the language exposed to a child [23,24]. Chomsky highlights that a dramatic and perhaps unique event in human evolutionary history produced UG in one leap [25], whereas other nativists advocate that each element of UG could have its own adaptive function and the whole evolved gradually from a series of naturally-selected changes [26,27].

The syntactocentric structure of language is challenged by the parallel architecture of language proposed by Jackendoff [28]. Jackendoff states that independent combinatorial principles exist not only in syntax but in semantics and phonology. Structures from the latter two components are connected via interface rules and perceptual systems. Instead of being passively manipulated by syntactic derivations, the associations between phonological, syntactic, and semantic features are an active part of the interfaces among these components. This parallel architecture repositions syntax in the language system, restates the relationship between linguistic components and general intelligence, and gains support from recent evidence of language processing capacities [29].

It remains unclear what kind of capacities constitute UG or FL per Chomsky's theory [30]. On the one hand, comparative evidence has revealed that many presumably language-specific mechanisms abound in many species, at least

as precursors [31]. For example, bees [32,33], dolphins [34], monkeys [35] and chimpanzees [36] can all grasp simple objects and their physical parameters, and master abstract concepts like sameness and difference. A border collie can learn to map the labels of over 200 distinct items [37]. Free-ranging putty-nosed monkeys can combine vocalizations into different call sequences linked to specific environmental events [38], and female baboons can modify their call production in various social contexts and towards different audiences [39]. Wild chimpanzees can acquire serial orders based on statistical information [40]. Captive bonobos, after language training programs, can respond to a variety of verbal commands having simple syntax [41,42]. In addition, many acoustic-perceptual features of human speech are not species-specific, but can be acquired by other animals [43]. For example, many songbirds can learn to respond to acoustic parameters conveyed in speech, such as vowels, voice onset time, and prototypical phonological categories [44,45]. Chinchillas [46] and baboons [47] can perceive conspecific calls categorically. Furthermore, many species are sensitive to statistical regularities in the input (within different modalities and domains) and apply general statistical mechanisms in learning activities. Such mechanisms are claimed to be important for language acquisition [48–51]. For instance, cotton-top tamarins can detect transient probabilities among syllables in utterance [3], and crows can understand causal relations [52] and conduct association learning by grouping visual stimuli based on meaning [53].

On the other hand, neuroscience evidence pinpoints that languages share neuronal components with vocalization in other species and other types of processing in humans. For example, dogs and humans share functionally analogous voice-sensitive cortical regions [54]. Broca's and Wernicke's areas, presumably the "seats" of language in the human brain, are also involved in music processing [55,56] and coordination of hand movements and vision [57]. Broca's area is frequently activated during language processing such as resolving syntactic ambiguity and sentence parsing [58,59] (see a recent review of involvement of Broca's area in language processing under the generative umbrella [60]). Nonetheless, this brain region has also been involved in non-linguistic tasks such as recalling items [61,62], identifying patterns of colors, shapes, or numbers of items [63], cognitive control of motor acts [64,65], and mathematical calculation [66]. Such co-involvement of Broca's area across different types of non-language specific activities indicates that this area could be a hub of the brain network that encodes hierarchical structures, regardless of their actual use across domains [67] (though see [68] for some counter-arguments). Moreover, although the left hemisphere of the human brain appears to be more active during linguistic tasks, a cooperation of both hemispheres has been recorded in linguistic tasks, such as reading English sentences having complex relative clauses [69] and processing fast- (e.g., stop consonants) and slow-changing (e.g., lexical tones) components during a lexical decision task [70]. Finally, structural homologs of Broca's and Wernicke's areas in some non-human species such as rhesus macaques are also activated during the presence of conspecific vocalizations [71] and the control of orofacial musculatures during vocalization [72].

Hauser, Chomsky & Fitch suggested separating FL into FL in a broad sense (FLB) and FL in a narrow sense (FLN) in order to clarify components of FL and their degrees of specificity to language [18]. FLB contains the sensorimotor and conceptual-intentional capacities, such as auditory channels, working memory, general intelligence, and shared attention, most being probably not specific to language and shared by humans and other species in different levels. FLN, by contrast, involves the capacities specific to language, and recursion is speculated as the only component in FLN (though see discussions on Pirahã [73,74]).

There had been some studies on recursion and its processing [75,76] before Hauser et al. highlighted the uniqueness of recursion in the language system. After Hauser et al.'s work, a renewed interest in recursion has been shown in investigations on the relations between language processing and human cognition. For example, Gentner and colleagues report that European starlings could recognize the A^nB^n structure in song motifs resembling linguistic recursion [77], but linguists soon point out that these songbirds could adopt a nonlinear strategy to distinguish such structure [78,79]. In addition, Jackendoff, based on the evidence from visual processing, music recursion, and narrative structure of comics, claims that recursion is ubiquitous in human cognition; accordingly, it belongs to FLB, rather than a defining feature of language [28]. Furthermore, Levinson finds that unlimited recursion like center-embedding is more available as pragmatic construals in every language and evident more in dialogue or conversation structure than in syntax [80].

There are critical limitations in existing studies centering on the occurrence of recursion in various aspects of the language system and the learnability of such structure in humans and non-human species (e.g., [81–83]). First, there is a lack of corpus evidence on complex recursion in natural language syntax [76,84–91]. Levels of embedding used in actual language are highly constrained: there exists no evidence of unlimited recursion, and more than one level of embedding never occurs in actual speech. Recent experimental evidence based on South Slavic languages also reveals

that grammatical production of configurations like coordinate structures is actually in favor of linear over hierarchical structure [92]. Therefore, learning and processing mechanisms underlying recursion or other hierarchical structures are not much representative for discussing the general nature of language acquisition. Second, it is very difficult to know exactly how non-human animals encode language-like signals in their minds [78,93], and more investigations on whether the acquired language-like knowledge of non-human animals can be generalized to novel instances are needed [94,95] (see [42] for such experiments). Finally, the acoustic confounds in stimuli design have reduced the grammatical explanatory powers of many existing studies [96]. Therefore, rather than recursion, more informative studies should target more frequently-used structures that serve universally more important roles in language, and explore biological, physiological, and cognitive constructs that collectively allow humans to develop, learn and use these structures.

The above-mentioned comparative and neural evidence tellingly reveals that language shares considerable behavioral links with sensorimotor substrates and non-linguistic skills [97,98]. Language acquisition mechanisms are neither language-specific nor human-unique; rather, they are comprised of a set of domain-general abilities (cognitive skills not being specific adaptations to a task, but used in several or all different domains [99]), which are largely shared, albeit in different degrees, among non-human species [100,101].

This line of thought as presented above is consistent with the “tinkerer” view on evolution [102]. Evolution rarely produces novelty from scratch; instead, it works on what already exists by either providing a system with new functions or combining available systems into a more elaborate one. Similarly, the evolutionary process of language does not favor specific modules, but accomplishes the task by modifying pre-existing mechanisms [103]. Language can be viewed as a new machine built out of old parts [104,105]. Therefore, what we should ask is not whether recursion is language-specific or human-unique, but whether FLN is empty [30,85,106], or if anything is there, what it looks like and how it is derived through evolution. All these inspire us to reconsider the nature of language foundations and their relations to general cognition.

3. Socio-cultural environment is another foundation of language

Language builds upon and integrates not only biological (e.g., respiration, mastication) but also social behaviors (e.g., remembering, reasoning, and socializing). In addition to the biological capacity (i.e., the basic functions of physical organs and cognitive competences for processing linguistic materials), language also exists as idiolect (the idiosyncratic body of knowledge each individual uses to communicate with others, see [107]) and communal language (the consensus of idiolects arising in use or extrapolation of idiolects, based on which speakers in a population can communicate and understand with each other, see [108]). Such dual-existence of language [109,110] suggests that investigating language foundations should examine both the biological predispositions in individuals and the socio-cultural environment and dynamics in which language is acquired and used.

Contemporary generative theories, however, are mostly concerned with an ideal speaker in a completely homogeneous speech community, who knows its language perfectly and is unaffected by grammatically irrelevant conditions like memory and transmission errors (random or characteristic) (see [111] for discussions on the concept of ‘speech community’). For example, many nativists highlight language as an internal thinking tool, which tends to isolate speakers from the arena of language use and imply that language use cannot fundamentally influence internal properties of speakers [21]. Speakers, though having largely similar cognitive structures associated with linguistic communication, may not have the same “grammar” or knowledge of a language, and therefore, perfect communication is not always achieved. For example, since people are in different states of knowledge, one can never be absolutely certain from another’s behavior that one’s message has been understood as the way one intends; instead, one can only settle for degrees of certainty dependent on situations [28], which is more so during the early stages of language origin [31,94], acquisition [105], or contact [108].

Noting this, some scholars [109,112–114] argue that language use and socio-cultural factors can cast constraints on language, thus playing more important roles in language acquisition and evolution than biological predispositions. Instead of arising from genetic influences specific to language, language is shaped primarily by a variety of pressures including learnability [84,115], memory limitation [116], and constraints on structure [117,118], processing [86,119,120] and communication [121]. Per this view, language acquisition is a task of integrating and coordinating multiple sources of information to fulfill communicative goals [122,123]. The ease in language acquisition is not because children possess innate linguistic knowledge or language-specific predispositions, but because the languages they

learn have evolved to fit in with the guesses children are likely to make [124–126]. During language evolution, it is language that evolves to be adaptive, rather than that humans evolve to be adaptive for using language [124]. Self-organization (a process whereby patterns at the global level of a system emerge from numerous interactions among the lower-level components of the system [127]) and domain-general learning mechanisms, such as imitation [105,128,129] or statistical or associative learning [130], are sufficient to induce and spread linguistic features and behavioral patterns among group members to establish a shared communication system [131,132].

Along with empirical investigations of language learning, recent psychological experiments have begun to study the emergence of a novel communication system resembling language in a laboratory setting [133–135]. Referred to as experimental semiotics, these studies often revolve around some language games [136]: Participants (typically dyads) are given a joint task that requires coordinating their actions, and a direct way to do so is to interactively build a communication system employing available means and media. In such games, subjects respond by adopting various non-linguistic and linguistic signals encoding simple lexical or phrasal meanings but typically lacking complete syntactic features of a real natural language.

Many experimental semiotics studies (e.g., [136–143]) implement a scenario of iterated learning (a process whereby an individual acquires a behavior (or language) by observing a similar one performed by another one who learns the behavior in a similar way [144]). In the experiments, a group of human subjects form a transmission chain [145], mimicking cross-generation cultural transmission in human communities with one or many individuals representing one generation. An individual's task is to learn an artificial language (or develop a novel signaling system from scratch), and externalize their knowledge of it. After learning, what one or some individual(s) produced is sent as input for learning to the individual(s) at the next position of the chain. Under this setting, individuals need to generalize their knowledge to express salient meanings, because no one receives all instances produced by the one(s) in the previous generation. Transmission bottleneck as such makes language learning inductive: A person induces his/her knowledge of what the language looks like and how it works based on the utterances from which that person learned the language [146].

Many iterated learning studies show that due to transmission bottleneck, a random signaling system gradually transforms into a communication system displaying principal linguistic properties such as compositionality (meanings of complex expressions are derived from the meanings of their components and the ways in which the components are combined) and regularity (various yet largely consistent ways of combining components into lexical items, phrases or sentences to express complex meanings). Most importantly, these universals rely on little biological predispositions (e.g., sequence memory constraint [147]), and emerge in both sophisticated linguistic signals and simple non-linguistic signals in the forms of pictures [148], moving patterns [149], whistles [150], iconic gestures [151], meaningless shapes [152], consonant strings [147], and so on.

Similar findings have been reported in computer simulations, especially agent-based models. These models are designed to address how iterated interactions among autonomous entities (agents) gradually lead to collective behaviors at the population level (see [153–155] for an overview). In a typical agent-based model investigating language evolution, each agent is equipped with a set of predefined or evolvable mechanisms that enable interactions with other agents. Similar language games can be defined in agent-based models as communication scenarios [109]. By manipulating the learning mechanisms and the ways of socio-cultural interactions among agents, these models can simulate various phenomena in the human socio-cultural environment.

Agent-based models and laboratory experiments provide complementary sources of evidence: Human experiments have the advantage of providing convincing evidence that something emerged in humans through cultural evolution; and simulations allows conducting or repeating experiments in a constructive and controllable environment to elaborate or evaluate hypotheses or evolutionary processes about a phenomenon that is hard to observe empirically or impossible in humans or animals. For example, simulations based on artificial agents help to avoid the influence of real individuals' prior linguistic knowledge on learning novel signals. In most laboratory experiments of human subjects, it is almost impossible to tell whether the subjects ever apply their pre-existing, highly overlearned natural language knowledge to produce language-like structure(s). In many iterated learning experiments, it remains unclear whether it is iterative learning and transmission bottleneck that lead to language-like structure, or it is simply iterative learning that induces subjects to tap into language structures they have already known. The smart setting of some recent experiment (e.g., [147]) can avoid this, but in the absence of communications. Recruiting pre-linguistic children and using carefully designed non-linguistic signals may partially avoid this, but incur additional difficulty in experimental design and other uncontrollable factors. Second, there are very few iterated learning experiments on non-human

animals [137,156,157], and strictly speaking, laboratory experiments on modern humans cannot reveal how language originated from the very beginning, since modern humans already have fully-fledged brains and cultures, thus making them incomparable to our pre-linguistic ancestors or non-human cousins in certain aspects relevant for language acquisition. By contrast, artificial agents in simulations can be constructed with a limited scope and degree of abilities to evaluate whether these preliminary learning and/or interacting mechanisms are sufficient to trigger a language-like communication system. Third, simulations allow explicitly tracing language acquisition at both the individual and community levels, and scaling up or down the limited time spans of laboratory experiments. Existing models can be readily expanded to new goals, making them flexible for extension and mutually understandable and supportive [158,159]. These characteristics render simulations a useful tool in addressing issues of language evolution. Existing agent-based and connectionist simulations (e.g., [107,160–166]) have implemented language transmissions among or between individuals of the same or different generations, replicated the roles of transmission bottleneck in shaping language structures, and illustrated separate and collective effects of different types of language transmissions on this process.

Christiansen & Chater propose that in addition to the transmission bottleneck, the “now-or-never” bottleneck during linguistic communications (while hearing a sentence unfold, we lose the memory of preceding materials rapidly) helps to construct language into a multi-level representation system [86]. This system requires deploying available information predictively to resolve possible ambiguities at different levels instantly, due to the impossibility of recovering previous information in this situation. This “chunk-and-pass” and “local-to-global” processing helps to interpret universal linguistic properties like duality of patterning (existence of one or more levels of symbolically encoded sound structure from which morphemes and words are composed) and language change principles like lexical diffusion (sound change originates from a small set of words and spreads to other words with a similar phonological make-up [167,168]).

The socio-cultural transmission of language serves as an arena for individuals to develop and acquire language, as shown in recent anthologies [145,169]. In addition to traditional empirical investigations, recent simulations (e.g., [107,146,162]) have demonstrated that basic language components such as lexical items and simple syntax can be acquired in an iterated learning setting by employing domain-general capacities such as sequential learning (the ability to detect and encode relative orders of discrete elements in a temporal sequence [170]), pattern extraction (the ability to detect and encode isolated or concatenated items repetitively occurring in linguistic or nonlinguistic instances [171]), and simple categorization (the ability to group items exhibiting similar patterns and apply available knowledge to newly-categorized items [113]). This echoes the stance that domain-general abilities are sufficient to develop and learn a communication system similar to language [131].

Socio-cultural transmission of language helps to explain typological bias and diversity in linguistic structures, resolve ambiguity due to flexible structures, and predict language shift. For example, corpus studies based on thousands of world languages have revealed that: the six possible forms of basic constitute word order (the most frequent relative order of subject (S), object (O), and verb (V) in simple declarative sentences) [172] are distributed in a biased fashion among world languages, in which the orders SVO and SOV are the most frequent ones [173]. Gong, Minett & Wang’s agent-based simulations demonstrate that individual processing constraint during communications (e.g., to understand a meaning involving animate action instigators and entities that undergo actions, one needs to explicitly distinguish object and subject) may select such orders in emergent artificial languages [174]. Dunn and colleagues show that socio-cultural factors are the primary determinant of word order [175]. Typological analyses of world language databases (e.g., [176]) further reveal that diversity is evident at almost every level of linguistic organization and it is mainly caused by socio-cultural and historical factors, as well as constraints from human cognition [177].

According to Lenneberg [1], humans possess biological predispositions enabling the production of a rich set of vowels and consonants. To interpret the displacement of vowels or consonants in specific languages, one also needs to refer to the socio-cultural environment of language. In addition to decades of sociolinguistics research of language use in its natural environment [178,179], simulation studies elaborate that the self-organization of vowels in production and comprehension helps to shape the vowel systems of different languages [180,181]. By modifying de Boer’s model [180], Chirkova & Gong trace a vowel chain shift evident in a dialect of a minority language in China [182]. This study confirms the fieldwork observations that the shift was due to contact between that dialect and Southwest Mandarin and borrowing of a vowel from Tibetan.

Decades of language documentation work has accumulated an abundant set of contact-induced language shift occurring in Africa, Europe, America (and elsewhere). Socio-cultural and socio-economic factors (e.g., speakers’

social properties, population size, colonization, and globalization) play important roles in inducing and driving these shifts [108,183]. These micro-historical pressures operating during transmissions to learners and interactions with communicative partners serve as the engines for constructing the language system and inducing changes observed at both the meso- and macro-historical scales [169,184]. In addition to documentation, mathematical models that transform the course of language communication into abstract equations [154] have also been designed to examine the roles of socio-cultural factors in language contact and language shifts thus induced [185,186]. For instance, statistical physicists [187] have proposed a mathematical model of language competition (the process whereby local tongues are being replaced by hegemonic languages due to population migration and sociocultural exchange; it is a typical type of language contact [188]). It defines diffusion equations using population sizes and prestige values of competing languages to determine transitional probabilities from using one language to using the other and vice versa. Assuming a direct shift from one language to the other, this model ignores bilinguals, an important intermediate state in most cases of language competition. Later models have modified this simple model by incorporating the bilingual state and discussing its role in preserving endangered language during competition [189–192].

The simple model and many follow-ups keep using the parameter of prestige to reflect the socio-economic statuses of competing languages via the parameter of prestige, and estimate the value of prestige via post-hoc curve fitting. This single parameter provides no clues about how various socio-economic factors collectively determine the prestige of a language and the dynamics of language competition. A recent model [193] dissects the prestige of a language into impact (influence of one language upon the other(s) in the competing region after this language diffuses into this region) and inheritance (attractiveness of a language during learning), and proposes the diffusion and inheritance principles to quantify these parameters based on the socio-cultural properties such as the sizes of monolingual and bilingual populations and the geographical distances between the region of competition and the population centers of competing languages. Using such empirically estimated parameters, this modified model can not only replicate many historical cases of language competitions (e.g., the English–Gaelic and English–Welsh competitions in UK), but also make reasonable predictions to ongoing competitions that lack sufficient empirical data (e.g., the English–Chinese and Chinese–Malay competitions in Singapore). Work of this kind can provide a better understanding of how various socio-cultural factors collectively influence the dynamics of language competition.

The aspects as discussed above demonstrate that in addition to biological foundations, socio-cultural environment is another indispensable component to understanding language, through its effects on shaping language components during acquisition or transmission and influencing the course and outcome of language shift.

Given that biological predispositions and socio-cultural environment are both foundational to language, a question naturally arises: What is the relationship between the two? To be specific, does one appear to be more important than the other in shaping language properties, or can language, as a cultural phenomenon, be isolated from the physical environment and biological infrastructure of language and speech?

Some studies attempt to address this question by analyzing phonetic and phonological features of languages. For example, Everett and colleagues, based on a survey of the laryngology data of speakers of different languages, predict that complex tone patterns should be relatively unlikely to evolve in arid climates, thus indicating that human sound systems are adaptive and influenced by environmental variables [194]. Dediu & Ladd analyze a large database of world populations, and discover that the population frequencies of specific alleles of the genes involved in brain growth and development (ASPM and MCPH1) are highly correlated with the presence of linguistic tone [195]. This implies that the distribution of tone languages could be due to genetic variations among populations, but more investigations are needed to confirm such causation relation. Moreover, Dediu and colleagues examine the vocal tract anatomy and physiology across populations, and find that the inter-individual variation in these properties is not randomly distributed across populations [196]. Such biased distribution could explain the systematic differences in phonetics and phonology between languages.

Another domain of investigations of the relative roles of socio-cultural and biological constraints on language properties is the linguistic categorization of colors. Per this issue, the universalist hypothesis claims that the categories of visual sensory stimuli are determined predominately by perceptual primitives in the visual perception system in humans [197–199] or visual environment [200], and that cross-language categorization patterns are restricted by these properties [201]. However, the relativist hypothesis states that linguistic categorization results mainly from linguistic and socio-cultural factors [202–205] and forces like grouping perceptually-close stimuli has a loose effect on linguistic categorization [206,207].

Many approaches have been adopted to address this issue, such as psychological experimentation of color acquisition [208–212] and perception [213–216], neuroimaging studies of categorical perception of color stimuli [217–221], and agent-based simulations of color category development and spread [222–227]. These studies report contrasting results in support of either of the two hypotheses. This leads to a third view that perceptual constraints and socio-cultural transmission collectively shape linguistic categorization patterns of colors across languages [228,229]. In addition, most existing studies adopt stimuli from the same or neighboring color categories or stimuli from the one-dimensional hue space, thus insufficient to address color categorization in the three-dimensional perceptual space. More systematic investigations are needed to illustrate the relative roles of biological constraints and socio-cultural transmission in shaping cross-language color categorization patterns as evident in the World Color Survey [197,230].

4. Coevolution between biological predispositions and language

Given that both domain-general biological predispositions and socio-cultural environment are foundations of language, language must result from both biological and cultural evolution. Compared to cultural evolution, biological evolution generally unfolds over a much longer timespan. This fact causes many scholars to naturally believe that biological evolution must have produced a language-ready brain before the emergence of language, and that cultural evolution would then have kicked in and cast its influence mainly on language change (e.g., [231]). However, even if largely domain-general, language learning mechanisms evolved long before language, and they would presumably continue to evolve in concert with the cultural evolution of language; in other words, there should be no explicit “watershed” between biological and cultural evolution [94]. Instead of springing forth in its full splendor, language would have evolved “in a mosaic fashion” [232], with the emergence of semantics, phonology, morphology, and syntax all at different times and via different schedules (and with different components of each of these at different times and schedules). Following this line of thought, instead of highlighting determinant roles of either type of evolution, scholars have begun to advocate a coevolution (a term from evolutionary biology, which refers to a reciprocal or cooperative effect between two or more species or system components, see [233]) view towards language.

Deacon, for example, advocates a hypothesis of language–brain coevolution, in the sense that language structure must have arisen in a long and drawn-out coevolutionary process during which brain and language structures would have exerted selections on each other [115]. The symbolic reference (using arbitrary symbols to stand for something else) provided the selection pressure for the evolution of hominid brains; once a symbolic communication was possible, simpler languages would have created a selection pressure for bigger brains capable of using and extending languages. The subsequent extensive use of symbolic communication would have constituted a cultural niche [234], which keeps imposing selective pressures on human cognition and vocal systems, leading ultimately to the modern kind of language. Throughout this process, language has done most of the adaptation, and the brain has co-evolved accordingly.

Hurford also proposes a gene–language coevolution scenario [94,235]. He points out that much of language structure has no role in an internal system of thought representation; instead, language has an important role in an external system of thought expression, which includes communication. Individuals having more successful communications are assumed to have some sort of selective advantage, and thus produce more offspring than others. Consequently, the strategies leading to successful communications would become prevalent in subsequent generations. Such strategies would not necessarily need to be language-specific. In fact, many of them could serve similar roles in other communicative activities than language. Hurford proposes a series of language “seeds” or precursors (domain-general cognitive capabilities such as episodic memory, abilities to understand predicate–argument structures, transitive inference, subitizing, etc. [31]). These precursors, once adopted to language learning and communication, could help hominins to develop a language. Along with this process, the precursors themselves would become prosperous in human cognition, thus ultimately leading to a degree difference in language-related capacities between humans and other species.

Tomasello proposes a coevolution hypothesis between language and the cognitive skills associated with it: The set of functions of language and that of mechanisms making language possible coevolve and bootstrap each other into existence [113,236]. In particular, he describes a “cultural ratchet” effect [237]: The process of cumulative cultural evolution requires faithful transmission that can work as a ratchet to prevent backward slippage, such that the newly invented or adopted mechanisms can preserve their improved forms faithfully until a further modification or improvement comes along.

It is rather difficult to identify direct empirical evidence for these theoretical arguments, since language, especially speech, left no direct fossil record, and species having primitive languages have gone extinct [8,31]. Some linguists attempt to use pidgins and creoles as an analogy to language emergence (e.g., [238,239]). However, the complexity of such languages is open to discussion [240], and analyses on recent world wide empirical datasets (e.g., the Atlas of Pidgin and Creole Language Structures [241]) reveal that pidgins and creoles often emerged in a multilingual society in need of a lingua franca, thus not providing a comparable window of language emergence [242–244]. Other linguists study existent “primitive” language like the Nicaraguan Sign Language [245] or the Al-Sayyid Bedouin Sign Language [246] to gain insight on language evolution. However, the speakers of those languages do not start off at the same place as our pre-linguistic ancestors or our nonhuman cousins do [108], and the relatively short lifespan (several decades or so) of those languages makes it utterly impossible to discuss possible coevolution between language and relevant abilities.

In addition to linguists, other specialists – neuroscientists, anthropologists, and geneticists – have joined the endeavor of pursuing evidence of coevolution between language and human brain, behaviors, and genome. For example, Krubitzer finds a correlation between increased behavioral complexity and increase in the areas of mammal brains that mediate those behaviors [247]. Schoenemann and colleagues find that prefrontal white matter volume is disproportionately larger in humans than in other primates [248]. Schoenemann argues that, as with other regions of the brain, the size of the frontal lobe across species is proportional to the degree of elaboration of the functions underlying this region [249], and that such cortical specialization increases the potential ability to differentiate complex sensory information into diverse constituent parts [103,250]. Hauser and colleagues [95], in line with Lenneberg, suggest that a large brain itself is insufficient to indicate language capacity or competence. For example, autistics, who have significant problems in acquisition and expression of language, often have larger brains than healthy children and abnormal neural networks in early development [251,252]. This indicates that it is the connections between neurons in the brain that matter.

Based on clinical study, geneticists have located the FOXP2 gene in the human genome [253,254], which appears to be critically relevant to the human abilities to develop language. In addition, during the evolutionary lineage leading to humans, two amino-acid changes occurred in this gene after the recent separation of humans from the other primates and none on the lineage leading to chimpanzees. This indicates a strong selection on this gene presumably due to the need for developing increasingly fluent speech [255]. However, recent studies have revealed that mutation in FOXP2 might not directly affect speech or language; instead, it might simply affect general brain properties, such as grey matter volume [256] or cortico-basal ganglia circuitry [257], thereby influencing domain-general cognitive functions such as motor control and sequencing in humans [258] and other species like songbirds [259]. This gene also works as a transcription factor to up- or down-regulate DNA in many tissues (brain, lung, gut lining) at various times of development [260]. A recent study further shows that common allelic variation in FOXP2 is not associated with individual differences in language skills; instead, it is more closely related to domain-general skills like sequential learning [261]. All these suggest that the evolution of FOXP2 is neither a direct nor a sole indicator of the coevolution between language and human biological capacities.

Simulations, compared to the other approaches as mentioned above, have the advantages of recapitulating long-term evolutionary phenomena within a reasonable timespan and allowing arbitrary manipulation of possible causal factors to show their effects [154]. These enable simulations to illustrate in principle the possible coevolution between language and domain-general abilities.

Some simulations show that a strong universal property of language does not imply a strong underlying biological bias in humans; the repeated use and transmission of language in a population of agents having weak biases for that property can result, under the right circumstances, in the amplification of these biases, thus creating a strong emergent patterning of the resulting communicating system [126,140,165,205,262,263].

Gong & Shuai demonstrate that the ability to establish a common ground or shared intention during general communication can coevolve with the communal language of a community [264]. Cognitive abilities allowing a degree of shared intention have been evident in non-human primates, albeit with relatively lower levels [265], and a high level of this ability in humans has been argued to be a prerequisite for language [236]. Gong and Shuai’s model shows that artificial agents equipped with a low level of this ability can gradually develop a communal language through the dynamics of cross-generation transmission, and the initially-low level of this ability in the population is boosted and gets “ratcheted” up to a suitable level by which a high degree of linguistic understandability becomes possible among agents. In addition, by manipulating natural selection (selecting individuals having a high degree of linguistic

understandability to reproduce offspring, who inherit their parents' levels of that ability with occasional "mutation", i.e., slight increase or decrease in the level of that ability) and combining it with cultural selection (selecting individuals having a high degree of linguistic understandability to talk to language learning offspring), this model illustrates that natural selection is the primary driving force for the coevolution between language and shared intentionality, but cultural transmission is also indispensable for this coevolution to proceed. This study exemplifies one version of the cultural ratchet effect proposed by Tomasello, and reveals that such effect is possible under a combination of both biological and cultural evolutionary forces. In a follow-up study, Gong and Shuai demonstrate that language can also coevolve with memory capacity and limited memory capacity also drives the transition from a holistic signaling system to a compositional language consisting of lexical items and simple syntax [266].

These studies demonstrate that the need to learn and use a language might select for cognitive abilities like greater attention to verbal input and better memory. They also illustrate how domain-general language precursors gradually become language-relevant mechanisms during the coevolution between language and cognitive skills associated with it. Such coevolution may also explain other cultural innovations such as tool use [267].

Simulations as such render it possible to evaluate various proposed coevolutionary scenarios and understand the dynamics of coevolution. Laboratory experiments as discussed before could not replace such simulations, since the time span covered by the latter is much larger than that by the former, and most existing studies of the former type are based exclusively on modern humans already having well-developed capacities to process language or signals. In addition, what is shown in the simulations serves as an evolutionary explanation for the observed degree difference in language-related abilities between humans and other primates, and thus complements comparative studies based on modern humans and other existing species. Comparative research can only examine whether similar abilities are shared among humans and other species, and identify degree differences of those abilities therein. However, they cannot reasonably account for the observed biological or cultural differences, nor trace intermediate evolutionary stages of those abilities. Finally, the above-mentioned simulation studies highlight the importance of individual learning, biological evolution, and cultural transmission to language acquisition and evolution [146].

In addition to language, the culture-gene coevolution hypothesis has been widely discussed in research of animal behaviors [268]. Also called cultural evolutionary theory, this hypothesis claims that cultural and genetic evolution interact with one another and affect both transmission and selection, and that culture could more directly affect the evolution of traits, or even the making of species [269]. For example, it has been shown that natural selection helps to shape the processes underlying the use of social information in social insects [270]. Coevolution between culture and functional genes corresponding to cultural foraging behavior and habitat use could have led to the behavioral divergence in sea animals such as whales and dolphins [271–274]. Comparative analyses have revealed that the evolution of large brains, sociality, and long lifespans in primates has promoted dependence on culture, which in turn could drive further increase in brain volume, cognitive abilities, and lifespans [275,276]. In line with these studies and the existing simulations as reviewed above, research on coevolution between language and relevant cognitive abilities can enrich the set of evidence of gene–cultural coevolution and contribute to our understanding of the general relationship between language and its biological foundations in humans.

5. Conclusion

This article surveys recent attempts to investigate foundations of language, and their findings have explicitly shown that:

- (1) Biological capacities in humans for language acquisition and use are not language-specific but domain-general;
- (2) Socio-cultural environment is another important foundation of language that deserves further investigation;
- (3) Language could have resulted from a coevolution with biological capacities, just like many other behaviors of humans and nonhuman species.

These claims are open to debate, as shown in the reviewed studies. Rather than persuading readers to accept them, the current review aims to inspire further discussions and novel qualitative and quantitative investigations on the issues about the foundations of language and the relations between language and human cognition.

It is worth stressing that most of the findings reviewed here are obtained from a multidisciplinary perspective. Following Lenneberg's monograph, there have been numerous studies addressing language acquisition and evolution

from a multidisciplinary perspective, as demonstrated in recent monographs and anthologies (e.g., [277–290]) and the EVOLANG conference proceedings (e.g., [291–298]). Research in a variety of disciplines, such as human experiments and simulations, as well as other traditional disciplines like genetics, biology, anthropology, and so on, have joined the endeavors to study language evolution. However, due to inevitable limitations of those approaches [5], one needs to unify those approaches and findings obtained by different approaches, in order to form a global picture of language foundations [299]. This multidisciplinary perspective, in terms of incorporating and cross-checking the knowledge, approaches, and findings of a variety of relevant disciplines for language and cognition, can offer the best prospect for a comprehensive understanding of the nature of language and attract interested scholars from a variety of disciplines to devote their expertise into the study of language acquisition and evolution [123,299]. This perspective is much broader than what was advocated and practiced by Lenneberg in his seminal work 50 years ago, and we thus believe that it is an imperative issue in modern research of language evolution.

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