

Language evolution: consensus and controversies

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Why is language the way it is? How did language come to be this way? And why is our species alone in having complex language? These are old unsolved questions that have seen a renaissance in the dramatic recent growth in research being published on the origins and evolution of human language. This review provides a broad overview of some of the important current work in this area. We highlight new methodologies (such as computational modeling), emerging points of consensus (such as the importance of pre-adaptation), and the major remaining controversies (such as gestural origins of language). We also discuss why language evolution is such a difficult problem, and suggest probable directions research may take in the near future.

Language is one of the hallmarks of the human species — an important part of what makes us human. Yet, despite a staggering growth in our scientific knowledge about the origin of life, the universe and (almost) everything else that we have seen fit to ponder, we know comparatively little about how our unique ability for language originated and evolved into the complex linguistic systems we use today. Why might this be?

When Charles Darwin published his book, The Origin of Species, in 1859 there was already a great interest in the origin and evolution of language. A plethora of ideas and conjectures flourished but with few hard constraints to limit the realm of possibility, the theorizing became plagued by outlandish speculations. By 1866 this situation had deteriorated to such an extent that the influential Société de Linguistique de Paris imposed a ban on all discussions of the topic and effectively excluded all theorizing about language evolution from scientific discourse for more than a century. Fueled by theoretical constraints derived from advances in the brain and cognitive sciences, the field of language evolution finally emerged from its long hiatus as a legitimate area of scientific enquiry during the last decade of the twentieth century.

Considerable progress has been made since then, but the picture that is emerging is highly complex (see Box 1). Understanding language evolution poses many challenges for contemporary science. Here we provide a broad overview of the current state of the art, focusing on major points of consensus as well as the remaining controversies.

Major points of consensus

The necessity of interdisciplinary collaborations

One might expect linguists to contribute the most to research on language evolution, but this is not the case. In fact, most language evolution researchers do not have a background in linguistics, but instead come from one of many other disciplines within the cognitive sciences and elsewhere. Although this may be a legitimate cause for concern among linguists [1], it is perhaps better seen as a testament to the cross-disciplinary nature of the field of language evolution (see Fig. 1). Indeed, possibly the strongest point of consensus among researchers is that to fully understand language evolution, it must be approached simultaneously from many disciplines [1-5]. We must understand how our brains work; how language is structured and what it is used for; how early language and modern language differ from each other and from other communication systems; in what ways the biology of hominids have changed; how we manage to acquire language during development; and how learning, culture and evolution interact.

Thus, language evolution research must necessarily be cross-disciplinary in order to provide sufficient constraints on theorizing to make it a legitimate scientific enquiry. Nevertheless, most researchers in language evolution only cover parts of the relevant data, perhaps for the reason that it is nearly impossible to be a specialist in all the relevant fields. Still, as a whole, the field appears to be moving in the direction of becoming more interdisciplinary. Collaborations between researchers in different fields with a stake in language evolution (such as [5,6]) are likely to become increasingly more important.

Exploring language evolution through computational modeling

Another emergent area of consensus is the growing interest in using computational modeling to explore issues relevant for understanding the origin and evolution of language (see Box 2). Many researchers across a variety of different disciplines now either conduct language evolution simulations or refer to such work as evidence for particular theoretical perspectives. For example, modeling work has been used to inform high-level theories about BIOLOGICALADAPTATIONS (see Glossary) for grammar [7–10]

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Glossary

Agent: an artificial organism in a computational or robotic model (see also Fig. la in Box 2).

Biological adaptation: an alteration over generations of an organism's phenotype that makes it better suited for its particular environment. Biological adaptations show the *appearance of design* in that they appear to fit some task, however non-teleological explanations can be found for such adaptations, such as natural or sexual selection.

Cultural transmission: the mechanism by which behaviours persist over time by being acquired and performed by a number of individuals. There are many different mechanisms that can result in cultural transmission, such as imitation, direct instruction and so on.

Genome: the DNA sequence of an organism.

Genotype: the information encoded in some or all of an organism's genome. Grammaticalization: the process of linguistic change that leads to the formation of new grammatical structure. Grammaticalization in this sense includes the development of new grammatical items from lexical ones and, more generally, any kind of fixing of syntactic patterns. The development of 'gonna' (signaling future time reference) out of 'be going to' (which originally only indicated movement in space) is an example of grammaticalization.

Iterated learning: a specific kind of cultural transmission where the behaviour being transmitted is learned through observation of that behaviour, which in turn forms the input to other learners. Linguistic transmission can be seen as the principle natural example of iterated learning.

Learning bottleneck: the limited sample of utterances from which the language learner must try and reconstruct the language of her speech community. The term reflects the idea that languages, in order to persist, must be able to survive being repeatedly squeezed through the narrow bottleneck of observed behaviour, despite being potentially infinite systems.

Linguistic universals: Specific characteristics of language structure and use that hold across most languages of the world. For example, if a language has the verb occurring before the object as in English (e.g. 'eat sushi') then it will most likely also have prepositions (e.g. 'with chopsticks'); but if the verb occurs after the object as in Japanese then it is likely to have postpositions (e.g. 'sushi wo hashi_{chopsticks} de_{with} taberu_{eat}').

Phenotype: the physical manifestation of a genotype. Usually considered to be an organism, but may be extended to include the behaviour of that organism and the products of that behavior.

Phonetic gesture: a basic unit of articulatory action in which the articulators (tongue, lips, etc.) used for speech production are configured in a specific way to generate a particular sound.

Pre-adaptation: a biological change that is not itself adaptive but which sets the stage for subsequent adaptive changes. A pre-adaptation for language is a biological change considered to be necessary for the emergence of language. Semiotic constraints: universal constraints on symbolic communication originating from within that system due to the inter-relations between the symbols themselves (words) and what they refer to in the world. These constraints are neither biological adaptations nor the product of cultural transmission, but derive from the interplay between the symbols (similarly to the relationship between symbols in mathematics).

Sequential learning: the ability to encode and represent the order of discrete elements occurring in a temporal sequence, such as the sequences of sounds making up words or the sequences of words making up sentences.

or the emergence of language structure through CULTURAL TRANSMISSION [11–17], but also at a more detailed level, such as the evolution of PHONETIC GESTURE systems [18] or a neural basis for grasping as a precondition language based on manual gesture [19]. Models are useful because they allow researchers to test particular theories about the mechanisms underlying the evolution of language. Given the number of different factors that may potentially influence language evolution, our intuitions about their complex interactions are often limited (see Box 1). It is exactly in these circumstances, when multiple processes have to be considered together, that modeling becomes a useful – and perhaps even necessary – tool (but see [1] for cautionary remarks).

The role of computational modeling in language evolution research can be divided up into three rough categories: (1) Evaluation. Computational models, like mathematical models, have the virtue that they enforce explicitness in the formulation of an explanation. As such, they can act as a rigorous check that a particular explanandum actually does follow from a particular explanans. In other words, they can help researchers to identify hidden problems. In some sense, they allow us to create novel experiments to test under which conditions language evolves.

(2) Exploration. Computational simulations can be used (with caution) to explore the general ways in which explanatory mechanisms or theoretical constructs interact. In this mode, simulations can help direct us to new theories.

(3) Exemplification. Finally, computational simulations can be a valuable tool for demonstrating how an explanation works. They can augment verbal and mathematical theorizing to provide working models for pedagogical purposes.

Computational modeling thus provides a powerful new tool for the study of language evolution. However, it cannot stand on its own. It must take its place alongside theoretical considerations, mathematical modeling, experimentation, and data collection (e.g. linguistic, archaeological, etc.). For example, some computational models may eventually lead to mathematical models [16], or vice versa [20]. Computational models may suggest novel psychological experiments [21] and so on. We envisage that the interest in computational modeling is likely to increase further, especially as it becomes more sophisticated in terms of both psychological mechanisms and linguistic complexity.

Pre-adaptations for language

There is a general consensus that to understand language evolution, we need a good understanding of what language is. However, the field is divided over what the exact characterization of language should be, and in what terms it should be defined. Nonetheless, some agreement appears to be in sight regarding some of the necessary steps toward language. Specifically, there seems to be agreement that prior to the emergence of language some PRE-ADAPTATIONS occurred in the hominid lineage. There is less agreement about what these may have been, but one candidate that has been proposed by many is the ability to use symbols [1,11,19,22-25]. In this context, symbol use is typically construed as a capacity for linking sounds or gestures arbitrarily to specific concepts and/or percepts in particular for the purpose of communication. In addition, it has been suggested that the ability to relate these symbols to each other was a further necessary preadaptation for language [26]. Although there is evidence that nonhuman primates have some capacity, albeit limited, for using sequences of arbitrary symbols in captivity (for a review, see [27]), there is considerable debate over whether they use these symbols to refer things in nature. For example, it has been suggested that vervet monkey alarm calls [28] do not refer symbolically to snakes, eagles or leopards, but rather elicit differentially conditioned flee responses associated with the presences of these predators [29]. Similarly, the use of manual gestures

Box 1. The complexity of language evolution

Human language is unique in arising from three distinct but interacting adaptive systems: individual learning, cultural transmission, and biological evolution (Fig. I). These are all adaptive systems in that they involve the transformation of information in such a way that it fits some objective function. This is most obviously true for the case of biological evolution: natural selection is the mechanism of adaptation par excellence. Variations in the transmitted GENOTYPE (see Glossary Box) are selected for in such a way that the resulting PHENOTYPE best fits the function of survival and reproduction. Similarly, individual learning

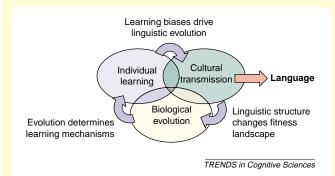


Fig. I. Language arises from the interactions of three adaptive systems: individual learning, cultural transmission, and biological evolution. A key problem for an explanatory theory of language evolution will be understanding how these systems interact on three different timescales: the lifetime of the individual (tens of years), the language (thousands of years), and the species (hundreds of thousands of years).

can be thought of as a process of adaptation of the individual's knowledge.

Less obvious is the notion of adaptation through cultural transmission (also sometimes referred to as 'glossogeny', see [57]). The knowledge of particular languages persists over time only by virtue of it being repeatedly used to generate linguistic data, and this data being used as input to the learner [3] – a type of cultural evolution termed iterated learning [58]. In this sense, we can think of the adaptation of languages themselves to fit the needs of the language user, and more fundamentally, to the language learner.

When we talk of language evolution in the broadest sense, therefore, we are referring to evolution on three different timescales [57,59]: the lifetime of an individual, a language and a species. What is particularly interesting about language, and why its emergence on earth can be seen as a major transition in evolution [60], is that there are interactions between all three of these systems (see Fig. I). The structure of the learner is determined by the outcome of biological evolution. Similarly, the pressures on linguistic transmission are determined in part by the learner's genetically given biases.

The final interaction is less obvious, but is the focus of much current thinking on language evolution. If there is some feature of language that must be acquired by every learner, and there is selection pressure on the reliable and rapid acquisition of that feature, then a learner who is born already knowing that feature will be at an advantage. This is the fundamental mechanism of genetic assimilation or the 'Baldwin Effect' [61] whereby learned behaviors can become innate. This, along with mechanisms such as niche construction and sexual selection, need to be understood before we can have a complete explanatory model of the evolution of language.

for symbolic communication in the wild has also been called into question [2,30]. Thus, the use of complex sequences of symbols referring to objects and situations may be a uniquely human ability.

Several other possible candidates for language-preadaptations have been put forward, of which we mention a few relating to changes in social or cognitive abilities here. Joint attention – that is, the capacity to follow eye-gaze direction or direct the attention of another to a specific object – is important for successful communication, and may have been a social precondition for language [2,22]. Another potential social pre-adaptation for language is the capability of modern humans for sophisticated imitation of action sequences for the purpose of communication [19,31]. Our ability to represent others as intentional beings with their own beliefs and desires, which can be manipulated by our actions, may also be a social prerequisite for language [2,31]. At the cognitive level, an increase in the capacity for representing complex concepts and combinations thereof may have predated the emergence of language [32]. Additional cognitive pre-adaptations that may have paved the way for language include the ability for complex hierarchical learning of sequentially presented information [3,5,27] and increases in the memory for sound sequences [33], both of which are important for the learning and processing of language. It should be noted, however, that many of the pre-adaptations mentioned above are shared with other species, in particular other primates [5,25], and that differences in these skills may be more quantitative in nature than qualitative.

Remaining controversies

Biological versus cultural evolution

Of course, several major points of disagreement still remain. Even though there is considerable agreement about a possible symbolic pre-adaptation among our hominid ancestors prior to the emergence of language, opinions differ considerably about the subsequent evolution of grammatical structure.

One line of theorizing suggests that grammatical structure is a consequence of an evolved innate grammar. There are several different proposals about why a biological adaptation for grammar may have evolved in the hominid lineage by way of natural selection. One suggestion is that language evolved gradually as an innate specialization to code increasingly complex propositional information (such as, who did what to whom, when, where, and why). This may have been for the purpose of social information gathering and exchange within a distinct 'cognitive niche' [7,34] or for a kind of social 'grooming' at a distance in groups of hominids too big for establishing social cohesion through physical grooming [8]. It has furthermore been argued that we in the many peculiarities of current language can find 'fossils' of prior, more primitive stages of language [24]. Another perspective suggests that grammar emerged more rapidly with the speciation event that produced modern humans some 120 000 years ago [1]. Common to most of these proposals is the suggestion that language syntax shows evidence of complex design - similar to, for example, our visual system [7] - and

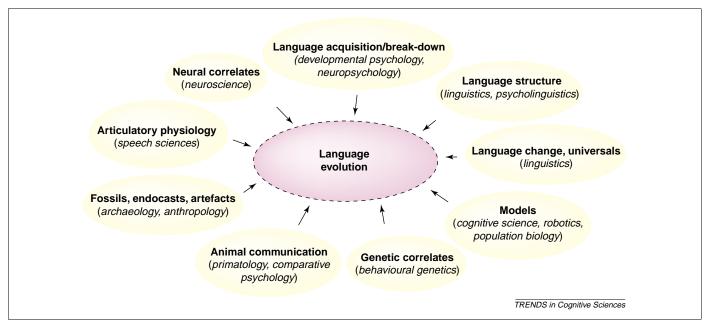


Fig. 1. The interdisciplinary nature of language evolution research. To home in on a full understanding of language evolution we need to draw on a huge range of data, and consequently, the expertise in a huge range of fields. This diagram shows the sorts of evidence that we need to look at, and the subject areas that are most associated with each. It is clear that an account of the origins and evolution of human language is an inherently interdisciplinary endeavor. Ultimately, we need to break down the barriers between each of the disciplines and be ready to look at the wider picture where possible.

that biological adaptation is the only way to explain the appearance of such design [10,34].

A different line of theorizing sees grammatical structure not as a product of biological adaptation, but as emerging through cultural transmission of language across hundreds (or perhaps thousands) of generations of learners. Language systems are argued to have grown increasingly complex due to the process of transmitting language across generations through the narrow filter of children's learning mechanisms. The way in which words can become crystallized into specific grammatical forms through GRAMMATICALIZATION (such as 'is going $to' \rightarrow 'gonna'$) is said to provide evidence for this perspective [22,32,35,36]. Other evidence comes from computer modeling of cultural transmission ([12-14] see [37] for a review), the development of indigenous sign languages [17], and the archeological record of artifacts [23]. Many proponents of the cultural transmission view of language evolution argue for a 'culture-first' perspective in which language evolved only after basic competences for relatively complex social culture had emerged in the hominid lineage [19,22,23,31]. However, additional constraints would seem to be needed if the appearance of design in language is to be explained [38]. Such constraints may be found in the limitations on our ability for SEQUEN-TIAL LEARNING of hierarchical structure [3,21], in the LEARNING BOTTLENECK created by forcing languages through the limited channel of children's learning mechanisms [39], in SEMIOTIC CONSTRAINTS governing complex symbol systems used for communication [11], or in the complexities of our conceptual apparatus [32]. Alone or in combination these constraints have been put forward to explain the elements of language that give the appearance of design, such as LINGUISTIC UNIVERSALS [40].

Earlier we pointed out that language arises from the interaction of three different adaptive systems: individual

learning, cultural transmission and biological evolution (Box 1). This suggests that both biological adaptation and cultural transmission may have interacted in the evolution of language. However, our understanding of such interaction is complicated by the fact that the three adaptive systems interact on three different timescales: the lifetime of the individual (tens of years), the language (thousands of years), and the species (hundreds of thousands of years). Determining the exact weighting of these three components with respect to each other and the nature of their contribution is thus an important issue for future research in the evolution of language.

Language origin: speech or manual gesture?

Another strongly debated issue in language evolution research is whether language originated in manual gestures or evolved exclusively in the vocal domain. On the one hand, it has been proposed that because vocal communication in primates is largely affective in nature and with little voluntary control, language is likely to have emerged from manual gestures rather than primate calls [41]. In some versions of this account, the emergence of gestural language was predated by the evolution of a unique human ability for complex imitation [19,31]. The subsequent change from a gestural to a primarily vocal language has been argued to be due to either increased tool use coming into conflict with the use of the hands for linguistic gestures [41] or the 'recruitment' of vocalization through associations between gesture and sound [19]. The close relationship between manual gesture and a subsequently evolved sophisticated ability for vocalization (in the form of speech) is furthermore suggested to have left us with the uniquely human characteristic of righthandedness ([42] - but see also [43]).

On the other hand, critics of the gestural theory of language origins have argued that manual gestures suffer

Box 2. Computational simulation

Since the late 1980s [62] there has been a steady growth in work that augments evolutionary arguments with simulation models (see [37] for review, and the UIUC language evolution and computation bibliography: http://www.isrl.uiuc.edu/~amag/langev/).

These simulations draw from three main computational techniques:

Multi-agent modeling

Most computational models of language evolution aim to understand the behavior of populations through modeling individuals or 'AGENTS' (see Glossary Box). The precise structure of the agent in a simulation will be dictated by the particular theory of language evolution being tested, but typically, it will have at least some of the features in Fig. la. Usually, agents interact with other agents in a population model, which may be dynamic, with agents entering and leaving the population over time (Fig. lb). Agents are embedded in an environment constructed by the researcher. It is this environment that determines the social interactions of agents and also what the agents will communicate about. A major research effort is currently underway to ground simulation research in real environments using robotic agents [63].

Machine learning

In Box 1, we noted that individual learning was one of the three key adaptive systems involved in language evolution. Unsurprisingly, many computational simulations model agents that acquire their linguistic behavioral competence through observation of such behavior (provided either by others in the population, or by the experimenter). There is a great deal of variety in the learning models employed, taking in a wide range of techniques from machine learning. These include connectionism [64], symbolic approaches (such as minimum description length induction [65], and instance-based learning [13]), and parameter-setting models [9].

Evolutionary computation

Many simulations of language evolution are concerned with the biological evolution of agents. In these models, some features of the agents are determined by an artificial genome. For example, in a connectionist simulation, the architecture of the networks may be specified by a set of parameters stored in each agent's genes [66]. These genes are subject to an artificial equivalent of natural selection, with the probability of their being passed on being determined by the 'fitness', of the agents that carry them. The details of how fitness is calculated are a key parameter for these simulations, but it is usually related in some way to success at a communicative task.

In many ways, these simulation techniques mirror the adaptive systems surveyed in Box 1. Some modelers focus primarily on biological evolution [67], cultural transmission [14], or individual learning [3], but increasingly, the simulation methodology is proving particularly useful for looking at how we can understand the interactions highlighted in Box 1 [9,12,68,69].

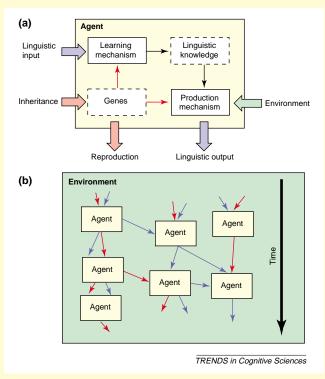


Fig. I. (a) A simulated agent. The architecture of a typical agent in a computational simulation. The agent learns from linguistic input, and uses the knowledge gained to generate linguistic output in response to some communicative need (e.g. by meanings being generated from an environment). In some simulations, the agent's architecture may be specified by an artificial genome that can evolve

(b) Biological and cultural evolution in a simulated population. In a multiagent simulation, a population of agents interacts and evolves. In this hypothetical example, genetic information persists over time through inheritance (red arrows), and linguistic information persists through repeated use and learning (blue arrows). The population is embedded in some simulated (or real) environment that will partially determine what the agents communicate about and their survival and reproductive success.

from two major disadvantages in comparison with spoken language: It requires direct line of sight and cannot be used at night [8]. Instead, several proposals have been put forward to support the possible origin of language in the vocal domain. One suggestion is that the basic structure of syllables derive from the succession of constrictions and openings of the mouth involved in chewing, sucking, and swallowing [44] - eventually evolving into phonetic gestures [33]. It has furthermore been contended that this evolutionary process may subsequently have resulted in the major syntactic distinctions between noun-phrases and sentences [45]. An alternative perspective suggests that natural selection for brain structures necessary for the motor activities involved in walking on two legs may have laid the groundwork for the evolution of the neural substrate necessary for speech production and perception, which in turn provided the basis for the emergence of syntax ([46] - but see also [5]).

Although mathematical and computational modeling may help inform the discussions about the relationship between biological adaptation and cultural transmission in language evolution, such modeling is less likely to be able to address issues related to the origins of language. However, evidence from other disciplines such as archeology, comparative neuroanatomy, primatology, psycholinguistics, and cognitive neuroscience may provide clues to an answer, though it is currently unclear whether this debate can ever be settled completely.

Future directions

One line of evidence that is likely to figure more prominently in future discussions of language evolution are results from the study of the human GENOME. A better understanding of the genetic bases of language and cognition, as well as its interaction with the environment during development may provide new constraints on

language evolution theories, in particular with respect to issues related to the origin of language. However, the relationship between language and genes is extremely complex [47,48], and the relationship between genes, language and evolution perhaps even more so [49]. Consequently, the current evidence provides few constraints on evolutionary theorizing. For example, data regarding the recently discovered FOXP2 gene [50,51] has been cited in support for very different theories of language evolution, ranging from a gesture-based perspective [41] to a speech-based perspective [46], from accounts involving large endowments of innate linguistic knowledge [7] to accounts eschewing such innate knowledge [46]. Nonetheless, there seems to be agreement that the *FOXP2* data [52] suggests a late evolution of speech. In this way, the genetic data may be particularly useful in informing our understanding of the timeline for language evolution.

Another type of evidence that may become increasingly important is data from studies that directly compare the learning and processing abilities of nonhuman primates with those of humans (either adults or children) using the same experimental paradigms. For example, comparisons of 8-month-old human infants [53] and cotton-top tamarins [54] on a simple artificial language learning task using the same preferential head-turn methodology indicate that both species may have similar abilities for basic statistical learning. Such work might allow us to better determine which components of language are unique to humans and which are shared with other species [5,22,55]. As a case in point, a recent review of this kind of comparative evidence regarding sequential learning suggested that an important difference between human and nonhuman primates is our superior ability for learning and processing hierarchically organized temporal sequences [27]. When combined with further corroborating evidence from neuropsychology and neurophysiology [46], computational simulations [3], and linguistic considerations [5] this human ability becomes a compelling candidate for a possible hominid biological adaptation that may eventually have led to the evolution of complex language. Future comparative research may reveal further differences that can inform our understanding of language evolution.

The challenge of language evolution

The recent and rapid growth in the literature on language evolution reflects its status as an important challenge for contemporary science. In this article we have given a whirlwind tour of some of the work currently being undertaken to answer this challenge. Our review has focused on the current trends and controversies in research on language evolution, and is aimed at providing a gateway into the primary literature where readers can delve into the many interesting details and perspectives that space did not allow us to cover here.

It is worth considering why language evolution poses unique problems for the disciplines involved. Language itself is rather difficult to define, existing as it does both as transitory utterances that leave no trace, and as patterns of neural connectivity in the natural world's most complex brains. It is never stationary, changing over time and

within populations which themselves are dynamic. It is infinitely flexible and (almost) universally present. It is by far the most complex behavior we know of – the mammoth efforts of 20th century language research across a multitude of disciplines only serve to remind us just how much about language we still have to discover.

There are good reasons to suppose that we will not be able to account for the evolution of language without taking into account all the various systems that underlie it. This means that language evolution is necessarily an interdisciplinary topic. There is inevitable skepticism regarding whether we will ever find answers to some of the questions surrounding the evolution of language and cognition [56]. Whether this skepticism is justified will depend on how well we can marshal the evidence and tools from all the disciplines reflected in this review. We hope that this article will go some way to making this possible.

Questions for Future Research

- Can an evolutionary approach help us discover innately determined features of language and whether those features are language specific? How does learning interact with evolution, and what implications does this interaction have for understanding innateness?
- What role does evolution by natural selection have to play in explaining language origins? What are the necessary and sufficient pre-adaptations?
- Can genetic and archaeological evidence converge on a timetable for the origins of language in hominids? What kind of evidence can resolve the gesture- vs speech-based origins hypotheses?
- How unique is human language? Does research in natural communication in other animals, and enculturated apes point to one, or many, features specific to humans? Is communicative function central to an evolutionary story or an epiphenomenon?
- Can computer simulation explain specific universal properties of language structure?
- What are the fundamental similarities and differences between cultural transmission and biological evolution?

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