

Title:

Multidisciplinary approaches in evolutionary linguistics

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Abstract

Studying language evolution has become resurgent in modern scientific research. In this revival field, approaches from a number of disciplines other than linguistics, including (paleo)anthropology and archaeology, animal behaviors, genetics, neuroscience, computer simulation, and psychological experimentation, have been adopted, and a wide scope of topics have been examined in one way or another, covering not only world languages, but also human behaviors, brains and cultural products, as well as nonhuman primates and other species remote to humans. In this paper, together with a survey of recent findings based on these many approaches, we evaluate how this multidisciplinary perspective yields important insights into a comprehensive understanding of language, its evolution, and human cognition.

Keywords

Comparative approach, FOXP2, Neuroimaging, Computer simulation, Psychological experimentation

1 Introduction

“The story of language evolution underlies every other story that has ever existed and every story that ever will.” (Kenneally, 2007, pp. 13). Understanding language evolution would doubtless provide the key to answering many related, yet unresolved questions, such as how world languages possess their distinct forms, why language is the way it is, and why only our species possess a complex linguistic system. These questions belong to the realm of *evolutionary linguistics* (Hauser et al., 2007; Fitch, 2010), which aims to identify when, where, and how languages originate, change, and die out (Ke and Holland, 2006). Due to the poverty of empirical data and limitations in methodology, research in evolutionary linguistics has long been suppressed ever since the *Société de Linguistique de Paris* imposed the ban on discussing issues concerning language evolution in scientific discourse in 1886 (Stam, 1976). Owing to the significant breakthroughs and rapid

development in computational powers, availability and reusability of abundant language corpora and database, and significant contributions from many other disciplines (Huang and Lenders, 2004), evolutionary linguistics has recently become a new beacon in modern scientific research to understand the nature of language and humans (Oudeyer, 2006), which can be vividly seen in many anthologies and reviews (Harnad et al., 1976; Hurford et al., 1998; Briscoe, 2002; Wray, 2002; Cangelosi and Parisi, 2002; Christiansen and Kirby, 2003b; Minett and Wang 2005, 2008; Tallerman, 2005; Hurford, 2007, 2012; Bickerton and Szathmáry, 2009; Larson et al., 2009; Tallerman and Gibson, 2012).

Language exists in two complementary aspects, namely language itself (in the form of idiolects and communal languages) and language users (in the form of the biological capacity for language) (Steels, 2005). Accordingly, research in evolutionary linguistics is also conducted in two lines, examining respectively the evolution of languages themselves and that of the biological capacity for language. The first line of research focuses on particular languages or groups/families of languages. Topics include, but are not limited to: (i) how to reconstruct the historical relations among groups/families of languages (e.g. the phylogeny of Sino-Tibetan, Indo-European, or Austronesian languages); (ii) how languages come into contact with each other in different socio-cultural settings (e.g. the contact or competition between dominant, invasive, or minority languages); and (iii) how phonological, syntactic or morphological features diversify across languages and change within languages (Evans and Levinson, 2009). By applying computational approaches from evolutionary biology and bioinformatics to the abundant language data (e.g., *World Color Survey* (Cook et al., 2005); *World Atlas of Linguistic Structures* (Dryer and Haspelmath, 2011); and *Ethnologue* (Lewis, 2009)), studies in historical linguistics and typology have been making significant contributions to these topics (e.g., Felsenstein, 2004; Wang and Minett, 2005; Atkinson, 2011; Huson et al., 2011; Levinson and Gray, 2012; Wang et al. 2012).

The second line of research focuses on *the faculty of language* (the set of capacities for mastering and using any natural language, Hauser et al., 2002). Topics include, but are not limited

to: (i) whether the generative capacity for language lies solely in syntax (Chomsky, 1986) or whether it can be evident in syntax, semantics, and phonology (Jackendoff, 2002); (ii) whether language processing abilities are determined by language-specific modules in the human brain (Pinker and Bloom, 1990) or whether they are derived from general cognitive abilities not initially specific to language or unique to humans (MacWhinney, 1999); (iii) how language processing abilities develop in children, allowing them to acquire particular linguistic structures; and (iv) how *linguistic universals* (particular features or principles of language structure and use that hold across most but not all world languages, Christiansen and Kirby, 2003a) originate, change and disappear.

Among these topics, *language acquisition* (the process whereby an infant acquires the ambient language, Clark, 2003) has been widely studied in psycholinguists, whereas *language origin* (the process whereby *Homo sapiens* made the transition from a prelinguistic communication system to a communication system with languages of the sort we use today, Wang, 1982; MacWhinney, 1999) has been largely restricted within a synchronic timescale, due to the fact that linguistic behaviors are hard to retrieve from fossil records (Hauser et al., 2002) and linguistics itself lacks scientific bases to evaluate language evolution in the past based on the data of the present (Ke and Holland, 2006). To overcome these shortcomings, studies in evolutionary linguistics, especially those concerning language origins, have to rely upon disciplines other than linguistics; that is to say, research in evolutionary linguistics is destined to be multidisciplinary. In this respect, evolutionary linguistics, and linguistics in general, needs to acknowledge the scientific approaches from other disciplines, comprehend their contributions to evolutionary linguistics, and conduct collaborative research with interested scholars from other relevant disciplines.

In support of this, we discuss in this paper a number of scientific approaches adopted in the study of language evolution. These approaches come from a variety of disciplines, including (paleo)anthropology and archaeology, animal behaviors, genetics, neuroscience, computer simulation, and psychological experimentation. For each approach, we list its primary assumptions,

review some of its major findings that contribute to our understanding of language evolution, and finally, point out its inevitable limitations and uncertainties.

2 Multidisciplinary Approaches to Evolutionary Linguistics

2.1 (Paleo)anthropology and archaeology

Approaches in these disciplines usually adopt two assumptions: 1) unique human behaviors including language could be determined by particular physiological and anatomical structures of humans; and 2) nonlinguistic phenotypes could provide indications of cognitive changes relevant for language evolution. Research of language evolution in these disciplines is often conducted in two ways: 1) comparing anatomically modern humans with fossils of extinct hominins to obtain evidence of the presence/absence of certain bony conformations associated with speech; and 2) examining archaeological records to find clues of every approximate levels of cognitive and social complexity of extinct hominins.

Though rarely touching on real language data, research in these disciplines can inform us of: 1) the evolution and migration of humans; 2) the correlations between linguistic behaviors and individual biological foundations and cultural activities; and 3) the rough time of the first appearance of language in humans. For example, by analyzing the skull endocasts of extinct hominins and modern humans, Schoenemann (2006) observed two changing tendencies of the brain size from early hominins to modern humans: 1) an absolute increase in the overall volume of the brain and 2) a relative growth of certain brain areas, such as frontal regions. Assuming a proportional correlation between the size of certain brain regions and the degree of elaboration of the functions that these regions underlie, Schoenemann ascribed the increase in brain size to the increase in the degree of specialization of certain brain regions, and pointed out that an increasing complexity of hominin conceptual understanding, manifest via the increase in brain size, led to an increasing need for syntax and grammar to perform efficient communications, thus driving language evolution. In addition, by examining tooth fossils of Neanderthals (an extinct hominin

species closely related to our ancestor, *Homo sapiens*), Smith and colleagues (2007) estimated the life history of this extinct hominin. During tooth formation, biological rhythms are manifest in enamel and dentine, creating permanent records of growth rate and duration. Analyzing tooth fossils can obtain a greater precision than analyzing skeletons, thus better facilitating the assessment of growth rates in hominins. This work revealed a shorter tooth formation period in Neanderthals than in *Homo sapiens*, indicating that a prolonged childhood and slow life history could be unique to *Homo sapiens*, just as other biological adaptations and aspects of social organization. Such a prolonged childhood is obviously beneficial for language acquisition.

Apart from human fossils, archaeological records of artefacts made by extinct hominins could also inform us of the origins and evolution of language. For example, D'Errico (2001) analyzed the knapping techniques for making stone tools, which required planning and significant skills, and hypothesized that: 1) the cognitive abilities supporting such tool-making activities provide tool-makers language-ready brains, i.e., capabilities to do a hierarchical thinking and a syntax-like organization of series of actions; and 2) the need to instruct tool-making in succeeding generations could drive the emergence and change of language. In addition, archaeological records of the habitats of early hominins could also indicate linguistic and other survival abilities of early hominins. For example, Coupé and Hombert (2002) analyzed the sea-levels of Wallacea region within the borders of Indonesia 60,000 years ago. During this period and from this region, early hominins first occupied Australia. The sea-level data showed that reaching Australia at that time required several times of sea-crossing, each at least 90 km wide. Apart from preserving sufficient food and drinking water or building strong rafts to bear difficult conditions in the open sea, such sea-crossing activities are impossible without a sophisticated communication system to share motivations, plans, and common goals among individuals. Therefore, the successful achievement of these sea-crossing activities indirectly elucidated that early hominins living during that period of time already had a language-like communication system.

All these studies reveal that: 1) language evolution, especially origin, reflected an intricate history of physiological, cognitive and social evolutions; 2) linguistic abilities could leave traces in nonlinguistic activities; and 3) analyzing such activities and associated artefacts could give us clues about the prerequisites for language, and when or where language first came into being in the human history.

Limitations and uncertainties: A large proportion of the studies in these disciplines rely on hominin fossils, associated artefacts, and other forms of indirect evidence. However, skull endocasts and bony formation reconstructed from hominin fossils provide less evidence of internal brain structure and how certain organs are operated in a living body. Insufficient evidence may lead to competing interpretations behind these records. For example, by comparing the larynx positions (via the hyoid bone to which vocal tract is attached) in modern humans, extinct hominins (e.g. Neanderthals), and nonhuman primates, Lieberman and Crelin (1971) suggested that the descent of larynx in modern humans enabled a flexible shape of vocal tract, which allowed producing a full range of phonetic contrasts, such as /i/, /u/, and /a/, thus making speech possible, whereas due to the unlowered larynx positions, other species failed to develop speech. However, new fossil evidence indicates that the hyoid bones in modern humans and Neanderthals were almost identical in size and shape (Arensburg et al., 1989). In addition, many living animals, such as dog, sheep or deer, are found to dynamically lower their larynx during vocalizations, and evolutionary biologists suggested that instead of speech, the primary reason for the descent of larynx could be size exaggeration (Fitch, 2010). Finally, based on computer-based phylogenetic reconstruction and ontogenetic data, computational linguists suggested that the potential vowel space of Neanderthal was as large as that of modern humans (Boë et al., 2002), and that infants, without having a low larynx, could still produce the cardinal vowels /i/, /u/, and /a/, and the cognitive capacity for motor control was needed for the origin of speech (Boë et al., 2007).

These recent findings show that: 1) the correlation between an anatomical structure and a function is not straightforward; and 2) having physiological apparatus doesn't necessarily imply

having the correspondent cognitive capacity. Therefore, in order to better elucidate language origins and evolution, (paleo)anthropology and archaeology call for support from other disciplines.

2.2 Animal behaviors

Studies in this discipline usually adopt a *comparative approach* (Oller and Griebel, 2004; Fitch, 2010), contrasting human behaviors with other animals' culturally varied behaviors, for the purpose of getting a sense of the likeliest range of behavioral or cognitive options early hominins could have taken (Balter, 2010). Since the biological evolution of humans often proceeds more slowly than the cultural evolution of language, the mental facilities of humans and other higher mammals are assumed to differ only in degree, but not kind.

Two lines of research are being conducted in this discipline: 1) identifying precursors of human linguistic abilities in our primate or ape relatives; and 2) analyzing shared features among humans and animals remote to us (e.g., dancing bees, songbirds, and oceanic animals), and comparing human language and the communication systems of those animals. There are three ways to conduct this research: 1) *field observation*, observing animal behaviors in the wild; 2) *wild or lab experiments*, doing experiments on captive or wild animals in labs or wild environments; and 3) *enculturation*, raising animals in a human environment with frequent human-animal interactions.

By a large-scale comparison among species, Fitch (2010) emphasized the importance of identifying *homology* (similar organic characteristics derived from a common ancestor) and *analogy* (similar organic characteristics evolving separately, not present in the last common ancestor) of language-related mechanisms. Homology helps pinpoint the origins of broadly shared traits in the hominin family, and analogy helps clarify cases where similar traits evolved independently in separate lineages, both offering clues of the evolution of language and linguistic capacity. Also by cross-species comparison, Hurford (2007) found that nonhuman animals possessed many linguistic precursors in the domains of semantics, pragmatics and syntax, such as episodic memory, representation of abstract properties, concepts or relations, transitive inference, and so on.

Through lab and wild experiments, Zuberbühler and colleagues examined the functional roles of the alarm/food calls in monkeys (Ouattara et al., 2009) and bonobos (Clay and Zuberbühler, 2009), and observed many language pre-adaptations in these species, such as combinatorial abilities, social awareness and shared intentionality. These findings indicate that during the recent evolutionary history of primates minor adjustments were sufficient to endow humans with language. In addition, Gentner and colleagues (2006) trained starlings to discriminate two types of birdsongs, one of which displayed an $A^N B^N$ structure resembling recursion in language. This finding triggers reconsideration among linguists about the uniqueness of recursive structures in language and relevant processing abilities in humans (Corballis, 2007; van Heijningen et al., 2009; Jackendoff, 2009). Furthermore, Grainger and colleagues (2012) trained baboons to use orthographic information to discriminate English words from non-word letter strings. This finding indicates that basic orthographic processing abilities could be grasped by nonhuman primates without pre-existing linguistic representations.

Through enculturation, Savage-Rumbaugh and colleagues (1998) examined the gestures and lexigrams used by captive chimpanzees or bonobos during interactions with human experimenters, and found that these animals could fluently use these communicative means to express their minds. They also observed some social skills in these captive primates, including pointing, turn-taking, and sensitivity to others' minds. Instead of primates, Pepperberg (1999) trained an African Grey Parrot named Alex to orally communicate with her. She reported that Alex could grasp not only simple concepts such as colors, shapes or matter, but also complex relations, second-order logic, role-taking in communications, etc. This research challenges the assumption that only humans possess those high levels of intelligence.

Limitations and uncertainties: In studies of language-like behaviors or abilities in nonhuman animals, there are inevitable gaps between language-like expressions acquired by animals and real languages used by humans, and between animals' behaviors and their inner representations of those behaviors. With no further means than behavioral recording, we have to interpret animal behaviors

based on our own thoughts, which may lead to biased conclusions. For example, cognitive linguist Corballis (2007) suspected that instead of a recursive rule, the starlings trained by Gentner and colleagues could simply use an iteration rule to distinguish the $A^N B^N$ structure. In order to convincingly demonstrate that an animal can master a recursive structure, one needs to show that the animal not only recognizes an $A^N B^N$ pattern, but also notices the nested relation between A and B, the latter of which is obviously hard based solely on the animal's performance.

In addition, since only humans develop language, there must be critical differences between human minds and animal minds (Hauser, 2010). Apart from similarities or precursors, studies of animal behaviors should also examine what are the crucial features defining humans and giving us language. For example, based on the comparative studies between infants' cooperative gestures and chimpanzees' intentional gestures, some linguists and psychologists (Corballis, 2002; Arbib, 2005; Tomasello, 2008) argued that the cooperative ability could be human-unique, leading to language only in the human lineage. The comparative approach alone is insufficient to systematically evaluate this claim, since most comparative evidence is based on modern humans and contemporary animals, which offers no direct clues of the intermediate evolutionary stages. Likewise, in order to comprehensively identify linguistic precursors in nonhuman animals, one needs to resort to other approaches than animal models to construe how these precursors step into language and gradually evolve into a language processing system in humans.

2.3 Genetics

A species' genome reveals its identity in biological evolution. The fundamental assumption in this discipline is that *genotype* (genetic constitution of a cell, an organism, or an individual) determines *phenotype* (observable characteristics of an organism). In the context of evolutionary linguistics, it corresponds to: human-specific changes in gene X contribute to human-specific changes in phenotype Y (e.g. particular linguistic behaviors). Apart from reconstructing the human lineage and

migration history via techniques from molecular genealogy, genetic research also helps identify the genetic basis of individual language behaviors.

Some widely-used approaches in this discipline are: large scale comparison, family aggregation, and twin studies (Stromswold, 2009). For example, by comparing a large sample of human subjects, geneticists identified the genetic deficits in human chromosomes associated with certain diseases, e.g., Williams Syndrome (WMS). This syndrome usually causes impaired mental, cognitive, and physical defects, but interestingly, linguistic competence and performance of WMS patients seem intact, indicating that general cognitive abilities and language development are dissociated (Bellugi et al., 1993) and there is a language-specific module independent of general cognition (Fodor, 2000).

The most striking finding in genetic research relevant for language evolution could be the discovery of FOXP2 (a particular gene located in human chromosome 7q, locus 31), based on a series of studies on the members of the KE family in London (Hurst et al., 1990; Fisher et al., 1998; Lai et al., 2001). Vargha-Khadem and colleagues (1995) reported that the affected members in this family, who possessed a mutated version of FOXP2, showed significant deficits in linguistic production (e.g. inability to form intelligible speech) and comprehension (e.g. deficits in processing words following grammatical rules, poor judgment of grammaticality). Apart from humans, variants of FOXP2 also present in chimps, rodents, birds, and other high mammals. By comparing the FOXP2 amino acids in humans, primates and rodents, Enard and colleagues (2002) found that the FOXP2 amino acids underwent two recent (<120,000 years) changes after humans diverged from chimpanzees. Since language also emerged recently in the human history, FOXP2 seems to be a 'language gene', selected particularly for language. Linguists Jackendoff and Pinker (2005) further claimed that the human version of FOXP2 is unique, constituting a central component in the genetic mechanism for encoding and developing the language faculty. Moreover, a recent molecule genetic study that introduced the two amino acid changes in humans to the endogenous FOXP2 of mice and compared these partially 'humanized' mice with wild-type ones showed that the humanized FOXP2

allele affected the basal ganglia in the mouse brain (Enard et al., 2010), suggesting that alterations in the basal ganglia circuits in the human brain are crucial for the evolution of speech and language.

Limitations and uncertainties: Genetic studies of language disorders require comparisons of a large amount of data. The scarcity of families with a large number of affected individuals would preclude geneticists from locating the responsible genetic loci. Meanwhile, it is also hard to collect a sufficient number of patients who suffer from a particular type of language disorder or a specific linguistic impairment.

In addition, a systematic study on the roles of particular genes in language development needs to take account of the findings in other disciplines, including psychology, physiology, and cognitive sciences. For example, as for WMS, a recent comparative study between WMS children and normal kids in various linguistic aspects, covering phonology, vocabulary, grammar and pragmatics, has shown that the language of WMS children is atypical in many aspects. For example, compared with normal kids, the development of the phonological speech perception in WMS kids is severely delayed; although WMS kids' performance on receptive vocabulary test is a definite strength, the advantage is not evident using other measures of vocabulary knowledge; the parallel deficits in visuospatial cognition and spatial language usage reflect the inter-dependency between language and general cognition; and WMS kids exhibit pragmatic anomalies in conversational interactions and narrative tasks (Brock, 2007). This comparison of multidisciplinary data shows little evidence that the linguistic skills in WMS children are selectively preserved.

Furthermore, regarding FOXP2, some extensive comparisons of language and cognitive skills between the affected and unaffected members of the KE family, and between the affected members and other aphasics showing similar speech and language deficits, revealed that the affected members suffered the most in the coding test, which corresponded to a core deficit in sequencing (Watkins et al., 2002). Such deficit underlies both the verbal and nonverbal aspects of disorder. In addition, some comparative studies also showed that mutated FOXP2 affected the coordination of complex song sequences in birdsongs (White et al., 2006), and caused synaptic connections in the

mouse brain to lose its plasticity, thus impairing motor learning (Groszer et al., 2008). This evidence indicates that the speech and language deficit in the affected KE family members could be attributed to a developmental disorder undermining motor learning and development, with concentration in the brain regions engaged in articulation and sequence learning. Furthermore, recent findings in genetics suggest that apart from controlling brain growth, e.g., striatum and cerebellum development (Fisher and Marcus, 2006), FOXP2 mainly acts as *a transcription factor*, regulating the expression of other genes. For example, we now know that FOXP2 can *down regulate* (turn down the expression of) CNTNAP2 (another gene located near FOXP2 in human chromosome 7, loci 35 and 36), and CNTNAP2 variants can cause a delayed speech acquisition in children (Poliak and Peks, 2003).

Combining the approaches and findings in genetics and other relevant disciplines, we know that: 1) the language disorder associated with mutated FOXP2 in the KE family does not support the existence of a genetically coded language module or faculty, and FOXP2 is not a language gene; and 2) the correlation between the human genotype and cognitive capacities is usually indirect, and such correlation cannot be reduced to simple correspondences between a single gene, or gene sequences and a specific cognitive repertoire (Clark and Lappin, 2011). Only by collectively investigating the role of multiple genes that operate at different levels of organ systems could genetic studies come closer to understanding of how speech or language works. In this respect, approaches from other disciplines, such as complex networks, would be necessary.

2.4 Neuroscience

Apart from genome, neural circuitry in the human brain is another type of empirical basis of human behaviors. Assuming that different brain regions are engaged in different actions, approaches in this discipline address language processing and evolution from a neural perspective.

The most popular approaches in this discipline are the neuroimaging techniques. By examining patients with neural damages or normal subjects during particular linguistic (e.g., attentive/pre-

attentive comprehension, covert/overt production) or psychological (e.g., nonlinguistic pattern recognition, attention shift) tasks, these techniques provide a new angle to observe human behaviors. Two widely adopted neuroimaging techniques are: 1) *EEG* (electroencephalography), using electrodes placed on the human scalp to record spontaneous brain activities over a short period of time during a linguistic or general cognitive task, it helps pinpoint the temporal reaction sequences of brain activities; and 2) *fMRI* (function Magnetic Resonance Imaging), measuring the BOLD (blood-oxygen-level dependence) signals due to neural activities in different brain regions, it helps locate the brain regions responsible for certain language processing mechanisms.

Based on a *violation framework* (comparing neural responses in processing normal language instances with phonologically, semantically, or syntactically incongruent instances), EEG-based studies have revealed different types of ERP (event-related potentials, i.e. the averaged EEG signals time-locked to a particular stimulus type or event) components that reflect phonological (e.g., P200, a positive-going ERP occurring ~200 ms after the onset of stimuli, Kong et al., 2010), semantic (e.g., N400, a negative-going ERP occurring ~400 ms after the onset of stimuli, Kutas and Hillyard, 1980), and syntactic (e.g., P600, a positive-going ERP occurring ~600 ms after the onset of stimuli, Hagroot et al., 1993) or morphosyntactic (e.g., LAN/ELAN, a negative-going deflection occurring around 100~300/300~500 ms after the onset of stimuli, Federici, 2002) processing in the brain (Kutas and Schmitt, 2003; Kuhl and Rivera-Gaxiola, 2008). These ERPs help verify or modify theories about certain linguistic phenomena. For example, binding anaphors (reflexive pronouns) with their antecedents is assumed to be a syntactic issue in linguistics (Reinhart and Reuland, 1993), but identifying antecedents in logophors (conjoined reflexive) remains uncertain. By recording subjects' brain reactions towards sentences with anaphor-agreement/-disagreement (e.g. *John's brothers like themselves/*himself.*) and logophor-agreement/-disagreement (e.g. *John's brothers like Bill and themselves/*Bill and himself.*), Harris and colleagues (2000) observed a P600 when comparing ERPs in the two anaphor conditions, but a P300 (a positive ERP occurring ~300 milliseconds after the onset of the reflexive pronouns, often triggered by some pragmatic processing)

when comparing ERPs in the two logophor conditions. These findings confirm that resolving anaphors requires syntactic processing, and suggest that resolving logophors needs semantics-related pragmatic or discourse processing.

By comparing brain activations across predefined conditions, fMRI-based studies have shown that Broca's area, anterior cingulate cortex, and other frontal regions in the human brain are crucial for coordinating different types of language processing (Grodzinsky and Santi, 2008). In addition, these studies have shown that certain brain regions, presumably as the 'seats' of language (e.g. Broca's and Wernicke's areas), are also activated in nonlinguistic activities, such as processing music (Maess et al., 2001) or coordinating hand movements with vision (Corballis, 2002), and that the neural substrate of speech overlap with that of nonlinguistic activities involving the body parts that express language (Pulvermüller, 2006). These findings reveal that language processing and nonlinguistic activities are correlated, in the sense that both recruit similar brain regions.

Limitations and uncertainties: These neuroimaging techniques also bear limitations (Luck, 2005; Logothetis, 2008). As for EEG, it fails to analyze the activations not time-locked, and its low spatial resolution restricts it from answering questions like: "where in the human brain are some linguistic features processed?" Meanwhile, compared with behavioral experiments, the functional significance of an ERP component is virtually never as clear as that of a behavioral response, and an accurate measurement of ERPs requires a large number of trials (Luck, 2005). As for fMRI, it uses indirect evidence (BOLD signals) to localize brain activations. Unlike its high spatial resolution, its temporal resolution is poor, since it has to take a few seconds after the task for the change in BOLD signals to be explicit. This makes fMRI unable to answer questions like: "when are certain linguistic features, semantics or syntax, processed during sentence comprehension?"

Apart from these technical limitations, it is not easy to design neuroimaging experiments that can efficiently prune irrelevant responses, sufficiently highlight responses of particular linguistic behaviors, and systematically compare linguistic and nonlinguistic activities. This leads to a debate in neuroscience studies, i.e., whether or not certain brain regions are selectively engaged in complex

perceptual and cognitive functions such as language. Some studies show that subjects' brain activations in nonlinguistic tasks (e.g. mathematical calculation, spatial working memory, stroop effects and music processing) do not overlap those in linguistic tasks (Saxe et al., 2009; Fedorenko et al., 2011), whereas others illustrate that frontal or prefrontal brain regions become activated in both linguistic and nonlinguistic tasks, such as music processing (Fadiga et al., 2009), calculation (Piazza et al., 2006), cognitive control of motor acts (Pulvermüller, 2006), working memory (Bunge et al., 2000), and multisensory integration (Braver et al., 1997), which indicate that language, as well as other cognitive behaviors, is a whole-brain function, sub-served by many brain regions that are involved in nonlinguistic activities as well. To resolve this debate, neuroscientists have to refer to linguistic theories for fine-grained design of linguistic tasks and approaches of other disciplines, such as computer simulation and complex networks (Sporns, 2011), for clear analysis.

2.5 Computer simulation

Computer simulation in evolutionary linguistics can be viewed as the operational hypotheses or theories expressed in computer programs (Parisi and Mirolli, 2007), and the results of these programs become the empirical predictions of the incorporated theories or hypotheses. There are two types of simulations: *behavioral models* simulate individual behaviors in linguistic communications and examine the roles of these behaviors in the emergent or acquired language structures; instead of actual behaviors, *mathematical models* transform language communications into mathematical equations, and predict the outcomes of linguistic activities based on the analysis on these equations.

Some behavioral models adopt artificial neural networks (ANN) to simulate language processing (e.g., Christiansen and Chater, 2001), which resemble, to a certain extent, the neural architecture of the human brain. In ANNs, neurons are organized into layers. *The input layer* receives the input signals, and propagates these signals, via the cross-layer connections (between the input and hidden layers), to *the hidden layer(s)*, which further propagates its(their) signals to *the*

output layer, also via the cross-layer connections between the hidden and output layers. The hidden layer is so called because the neurons in it have no direct interface with the input or output signals, and the output layer is so called because neurons in it produce the output signals, in response to the input signals. The weights of the cross-layer connections encode linguistic knowledge, and can be updated during *the training phase*. In each round of training, the ANN's output, in response to a particular input signal, is compared with a target value, and the difference between the target and actual output is propagated back to the hidden layer. According to this difference, the weights of the cross-layer connections between the hidden and output layers are adjusted so that the future output, in response to that particular input, will become closer to the target value. Similarly, the cross-layer connections between the input and hidden layers are also adjusted. Such weight adjusting process iterates in successive training cycles to improve the ANN's performance.

A particular type of ANN, *simple recurrent network* (SRN) (Elman, 1990), has been widely used in simulations of language processing and acquisition. In a SRN, apart from the input, hidden, and output layers, there is a *context layer*. Neurons in it copy the activation of the hidden layer in the previous time step, and determine the activation of the hidden layer in the next time step, together with the input layer in the next time step. Based on SRNs, Reali and Christiansen (2005) showed that the transitional probabilities between words were sufficient to solve *the auxiliary inversion problem* (when changing a declarative sentence with an embedded clause into an interrogative, which auxiliary, the one in the main clause or the one in the embedded clause, should be moved to the front? Boeckx, 2006). Other studies showed that SRNs could organize lexical items into a hierarchy of semantic classes, acquire grammatical relations, and handle subject-verb agreement in constructions containing several embedded relative clauses (e.g. Cartling, 2008).

These studies illustrate that: 1) language acquisition is not fundamentally different from other type of learning; 2) it can be accounted for by the same mechanisms used by individuals to interact with the environment in general; and 3) the general learning mechanisms can generalize sufficient knowledge from limited linguistic materials, thus challenging '*the poverty of the stimulus*'

arguments (the language data input to children are too limited, haphazard, and imperfect to allow children to infer the grammar of the ambient language without innate, language-specific learning mechanisms, Chomsky, 1986; Marcus, 1999). All these trigger *connectionism* (Christiansen and Chater, 2001; Elman, 2005), a school of thoughts on language processing, acquisition and emergence, in contrast to *innatism* (Chomsky, 1986; Pinker and Bloom, 1990).

Other behavioral models adopt *agent-based systems* (Bonabeau, 2002) to simulate language users (artificial agents) and their behaviors (predefined or evolvable mechanisms equipped by agents to handle linguistic materials) (e.g., Ke et al., 2002; Gong, 2009; Baronchelli et al., 2010). In a multi-agent system, agents can interact with each other, acquire and update their linguistic knowledge, and replace or get replaced by new agents. Linguistic knowledge on how to encode semantic expressions and decode utterances is simulated as rules. By manipulating communicative patterns or agents' identities, these systems can also incorporate socio-cultural factors and explore their effects on language evolution.

Some agent-based simulations defined *language games* (communicative situations in need of certain linguistic feature or structure, such as color terms, tense, or aspect, Loreto and Steels, 2007) to explore the cultural evolution of language (Steels, 2011). In order to successfully perform these games, agents gradually recruited necessary mechanisms to serve the communicative purpose and develop certain structures in their languages. Both the recruitment mechanism and adopted functions were not necessarily language-specific. These studies have shown that language evolves by recruiting cognitive operations for symbolic communications (Steels, 2009).

A well-known agent-based model exploring the roles of cultural factors in language evolution is the *iterated learning* (learning by observation of behaviors in others, and those behaviors themselves were also learned in the same way) model (Kirby, 1999). In this model, agents were organized in a chain, each denoting a language user from a generation. They were equipped with learning abilities to acquire grammatical structures and lexical rules to encode integrated meanings with simple predicate-argument structures (e.g., "love<Mike, Mary>"). The first agent in the chain

used a holistic signaling system to encode these meanings. It taught this language to the next agent by sending some meaning-utterance mappings it created. The next agent tried to acquire linguistic knowledge based on those mappings, and sent its meaning-utterance mappings to the next agent in the chain. This process was repeated along the chain, resembling cultural transmission across succeeding generations. During transmissions, a new learner may not receive all the meaning-utterance mappings produced by the agent in the previous generation. Such inevitable *transmission bottleneck* drove the initial holistic signaling system started to evolve into a compositional language consisting of combinable lexical items and regulating rules. Such language could be easily acquired from a small set of mappings, thus enabling it to pass through the transmission bottleneck. In other words, this model suggested that certain language structures (e.g., compositionality) could evolve as a consequence of cultural constraints (e.g., transmission bottleneck), which offers a new explanation on linguistic universals.

Apart from behavioral models, by analyzing well-established equations, mathematical models help reasonably predict some linguistic phenomena, such as language competition without (Abram and Strogatz, 2003) or with the bilingual state (Minett and Wang, 2008). These models used differential equations to describe the change of the populations speaking different languages, and the analysis of these equations helped reveal the stable states during language competition and the possible mechanisms causing the system to approach and reside in these states. In addition, mathematical models can also study the dynamics of certain linguistic features or behaviors. For example, Wang and colleagues (2004) presented a mathematical model studying the lexical diffusion (Wang, 1969) in a population of contacting agents. It assumed that at certain time step t , the frequencies using the unchanged and changed forms of a word could be calculated based on the corresponding frequencies at an earlier time step, $t-1$, and the use of the changed form was propagated by contact among pairs of agents, one of whom used the changed form and the other used the unchanged form. Under these assumptions, the model obtained a logistic curve tracing the frequency of the changed form in the population, and such S-shape dynamics matched the empirical

data of sound change in some Sinitic languages (e.g., Shen, 1997). By adopting the Price equation (Price, 1970) from evolutionary biology, Gong and colleagues (2012) analyzed the possible selective pressures for the diffusion of linguistic variants. This model reported that *the variant prestige* (the preference for using certain types of variants over other types in communications) could consistently drive the diffusion of preferred variants, whereas other factors, including the preference for certain individual(s) or various forms of social structures, only helped modulate the degree of diffusion when the variant prestige was involved.

Most mathematical models by now only focus on the general dynamics of some simplified systems and leave out some complexities, and it is generally difficult to establish a mathematical model to study the dynamics of a complex nonlinear system containing numerous factors and many interactions among these factors. Therefore, in order to get a comprehensive understanding on language evolution, covering elements such as individuals, their behaviors, and linguistic and nonlinguistic constraints, both behavioral and mathematical models are necessary.

All these simulation studies reasonably capture the complexities in linguistic structures, language users and socio-cultural environments, and reliably illustrate whether a minimal set of assumptions can parsimoniously generate the essential aspects of language and whether certain factors are crucial for language (Lyon et al., 2007). Both of these aspects help transform linguistic theories from a descriptive science into an explanatory one (Mareschal and Thomas, 2006).

Limitations and uncertainties: Simulations inevitably involve *simplification* (models tend to capture restricted features and abstract them too much to fully represent the original features in the real phenomena) and *specification* (a model often focuses only on particular factors most relevant to the incorporated theory or hypothesis). For example, many ANNs lack a semantic interface (Schalkoff, 1997). Models on syntactic evolution (e.g. Kirby, 1999; Gong, 2010) usually focus on a particular type of syntax, leaving out other grammatical structures. As a complex adaptive system (Beckner et al., 2009), language cannot be explained by single cause, factor, or function (Fitch, 2010), but it is impossible to address these many aspects at the same time and resolve them once for

all. Therefore, simplification and specification are necessary, via which the target complex question can be segmented and become explicit in subsets, sub-processes, and particular situations of the original system, and convincing conclusions obtained in those simplified and specific cases can eventually lead to a comprehensive understanding of the original question. Such ‘from simple to complex’ strategy and ‘divide and conquer’ componential approach are common in scientific investigations. However, an over-simplified model may miss the essence of the problem, making relevant factors for the target question trivial; an over-specified model leaving out other aspects but the target one may also cause the conclusions to be less significant, since ideal situations where one linguistic aspect is rarely affected by others are hardly possible in reality.

In addition, simulations only show what could happen, not what must have happened (Hurford, 2012). Due to lacking direct evidence and quantitative evaluation mechanisms, a direct comparison between the simulation results of language origins and the empirical data is not often possible. Resorting to techniques and findings in other disciplines helps overcome this uncertainty. For example, aided by neuroimaging technologies, simulation results of neural networks on language processing can be compared with the brain activation data obtained from neuroimaging experiments.

Furthermore, the implementation of a model usually involves many arbitrary choices, some of which are hard to abstract from reality. Any neglect of parameter setting, coding, or analysis may lead to either a mismatch between what one believes a model is and what it really is, or a mistake neglecting significant phenomena (Galán et al., 2009). In order to avoid these, we have to take explicit, justified, and plausible choices during model implementation, and adopt systematic methods during result analysis.

2.6 Psychological experimentation

This approach involves the design of human experiments to evaluate the effects of socio-cultural factors on language evolution and trace the origin of a sophisticated communication system in a population of human subjects (Scott-Phillips and Kirby, 2010). It has been recently adopted in

evolutionary linguistics, and undergoing rapid development, as shown in many recent language evolution conferences (e.g., Normile, 2012).

Kirby and colleagues (2008) conducted several behavioral experiments adopting the same cultural transmission framework as in the iterated learning model to examine the roles of the cultural factors on language evolution. In these experiments, a group of human participants were recruited to learn an 'alien' language. This fictitious language was created using a set of randomly chosen utterances to encode a number of images each having certain color, shape or patterning. For each participant, there were two stages: in the learning stage, via a computer screen, the participant was shown a sub-set of this language for memorizing; and in the testing stage, the participant was asked to type in appropriate utterances for a number of images appearing on the screen, some having color, shape and patterning combinations not shown to the participant during the learning stage. After these stages, some of the produced utterances of the participant, combined with the corresponding images, became the 'alien' language used to train the next participant in the line. These processes were repeated along the line of participants. Similar to the simulation results, the initial random language gradually became structured and easier to learn. By releasing the constraint of single-individual in each generation, new experiments set up multiple, communicating individuals in each generation to analyze the roles of vertical (as in the old experiment) and horizontal (as in the new experiment) transmissions on language evolution. Similar to the iterated learning model, these experiments highlight that cultural transmissions could shape language structures, without the need of strong innate biases for such structures in the language faculty.

Galantucci (2005) conducted another behavioral experiment focusing on the origin of a communication system from scratch. In this experiment, two participants were recruited to play a computer game. They were instructed to move their virtual agents into the same virtual room shown in the computer screen. In order to do so, they needed to communicate via a channel where most traditional means of communications, e.g., speaking or writing, became useless. Nonetheless, after a number of trials, these participants gradually developed a communication system based on a

conventional set of symbols to exchange location or movement information required in the experiment. Despite of their apparent differences, this novel communication system shared many features with language, e.g., both were conventional, tolerable for variations, compositional, parsimonious, and extendable. A later experiment (Scott-Phillips et al., 2009) extended Galantucci's work by removing the predefined communication channel, but letting such a channel to be gradually adopted by participants during the game. In this experiment, participants were instructed to move their virtual agents to the virtual rooms having identical colors. They could observe each other's movements on the computer screen, but not the colors of their partners' rooms. After some trials, these participants started to notice that the movement patterns could indicate communicative intentions and exchange information. By adopting movement pattern as a new communication channel, they developed a communication system capable of encoding the colors of their current rooms or the rooms they intended to move to. These experiments offer clues about how the human communication system originated and evolved, what were the prerequisites for such system to emerge (e.g., the meta-representation ability to notice that others' signals are intentional and contain communicative information), and what characteristics such system could have (e.g., it has to be explicit, conventional, and flexible).

Limitations and uncertainties: In these experiments, it is difficult to exclude participants' linguistic knowledge. For example, in Kirby and colleagues' experiments, the emergent linguistic structures could be an artifact from participants who already have language. In order to overcome this limitation, Verhoef and de Boer (2012) designed a new experiment, in which rather than fictitious language, participants were instructed to use slide whistles to produce whistling sounds to encode meanings, and the whistles produced by one participant were used to train the next one during cultural transmissions. After a number of learning and producing cycles, structural elements, such as low-high and high-low whistles, gradually emerged and were largely reused and combined to form new meanings, making this structural whistling "language" more learnable and reproducible. These results echoed and enhanced the conclusions drawn from Kirby and colleagues' experiments.

In addition, these experiments use modern human's performance to predict what could happen when early hominins developed their communication systems, but there could be mismatches in behaviors and cognitive competences between modern humans and their ancestors. In this respect, the fact that both the iterated learning model and relevant experiments show similar results becomes significant, since it supports each other's conclusions and a combination of simulations and experiments provides a plausible way to unravel problems of language emergence in history.

3 Conclusions

As discussed in previous sections, multidisciplinary approaches can make significant contributions to our understanding of language and its evolution.

On the one hand, these approaches can extend our vision on language and its evolution, and provide more useful and richer knowledge on language than what linguistics itself could bring about. For example, the neuroimaging techniques reveal the complex brain mechanisms behind linguistic behaviors and close correlations between linguistic and nonlinguistic activities. The genetic approaches lead us far back into history, surpassing the time limit that historical linguistics bears. The comparative data of animal behaviors help bridge the gap between humans' language-specific behaviors and animals' general competences. And the simulations and experiments recapitulate the major stages of language evolution and acquisition, and let us experience hundreds of thousand years of evolution within a short period of time.

On the other hand, the findings based on multidisciplinary approaches can pose critical challenges and reconsideration to traditional linguistics. For example, many animal studies and neuroscience findings have indicated that language-specific components may not exist in the faculty of language; linguistic competences in humans may derive from general cognitive abilities shared, though in different degrees, by other animals, and these competences also manifest in other cognitive tasks in humans' everyday lives. By simulations and experiments, we have discovered many powerful mechanisms used by children/adults during language acquisition. By computational

analysis, we have obtained better understandings of the available linguistic materials. And by neuroimaging techniques, we have traced detailed development and operation of neural modules in the human brain. All these inspire us to question some long-time dogmas in traditional linguistics, such as the assumption of the poverty of stimulus and the critical period in language acquisition. Noting the correlations among language, speakers, and socio-cultural environments, studies in historical/contact linguistics have to extend their visions, not focusing exclusively on linguistic materials. Similarly, more reasonable syntactic theories should not only describe abstract forms, but discuss whether humans possess relevant mechanisms to handle those forms. By viewing language as a complex adaptive system, a meaningful study of linguistic communications should take account of not only syntax, but also semantics, pragmatics and other relevant information. To sum up, many traditional linguistics fields need to reinvent themselves in order to accommodate multidisciplinary approaches. And only in this way can more meaningful understanding about language and its evolution be obtained.

Meanwhile, though shedding light on many aspects of language evolution (e.g., linguistic complexity, genetic and neural bases of linguistic behaviors, and socio-cultural environment whereby language is learned and evolves), these approaches also bear limitations and uncertainties. In this respect, in evolutionary linguistics research, cross-disciplinary collaborations are encouraged and sufficient guidance and support from linguistic theories and language data are necessary, both of which help avoid building in questionable assumptions, drawing conflicting conclusions, or paying attention to trivial factors. For example, the typological data of world languages reveal an essential similarity between Australian languages and other languages in the world and a high degree of phonological sharing between Australian languages and Austronesian languages in Southeast Asia. This evidence indicates that a separate language origin in Australia seems unlikely, thus supporting the conclusion of the study of sea-crossings (Coupé and Hombert, 2002). In addition, linguistic analysis of recursive structures could guide animal behavioral studies that aim to verify whether nonhuman apes can process particular types of structures (e.g., recursion) in a way

similar to humans, and the language acquisition data of normal and deficit human subjects can help comprehensively study the roles of certain genes or certain brain regions. Furthermore, by means of neuroimaging techniques, we can compare the brain activations during language processing with those during tool-making to analyze the correlation between language processing and tool-making, which helps verify the hypothesis of archaeologists about the evolutionary links between language processing abilities and tool-making skills (Stout and Chaminade, 2012). Finally, the language acquisition data can guide not only the design of processing and learning mechanisms of artificial agents in computer simulations, but also the analysis of the simulation results and human data obtained from the behavioral experiments of the transmission of an artificial language and the origin of a new communication system.

Noting these, we need to bring together diverse views/approaches to tackle problems about language evolution. In practice, we need to consider both linguistics studies describing various linguistic phenomena and proposing causation theories, and multidisciplinary approaches helping, from different angles, identify the mechanisms behind those phenomena, reveal the evolutionary trajectories of those mechanisms, and analyze or predict the outcomes of those mechanisms. Only a multidisciplinary perspective, based on pooled knowledge from diverse disciplines to reconcile seemingly contrary positions and rule out solutions plausible only within a single discipline, can lead to a biologically plausible, computationally feasible, and behaviorally adequate understanding of language and its evolution (Bickerton and Szathmary, 2009; Gong et al., 2010). As evident in the biannual EVOLANG conferences (Cangelosi et al., 2006; Smith et al., 2008, 2010; Balter, 2010; Scott-Phillips et al., 2012; Normile, 2012), such a multidisciplinary perspective has gradually become a default principle in modern linguistics research.

References

Abram, D.M., Strogatz, S.H., 2003. Modeling the dynamics of language death. *Nature* 424, 900.

- Arbib, M.A., 2005. From monkey-like action to recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences* 28, 105-124.
- Arensburg, B., Tillier, A.M., Vandermeersch, B., Duday, H., Schepartz, L.A. Rak, Y., 1989. A Middle Palaeolithic human hyoid bone. *Nature* 338, 758-760.
- Atkinson, Q.D., 2011. Phonemic diversity supports a serial founder effect model of language expansion from Africa. *Science* 332, 346-349.
- Balter, M., 2010. Evolution of language: Animal communications help reveal roots of language. *Science* 328, 969-971.
- Baronchelli, A., Gong, T., Puglisi, A., Loreto, V., 2010. Modeling the emergence of universality in color naming patterns. *Proceedings of National Academy of Sciences of USA* 107(6), 2403-2407.
- Beckner, C., Blythe, R., Bybee, J., Christiansen, M.H., Croft, W., Ellis, N.C., Holland, J.H., Ke, J., Larsen-Freeman, D., Schoenemann, T., 2009. Language is a Complex Adaptive System: Position paper. *Language Learning* 59(suppl. 1), 1-26.
- Bellugi, U., Marks, S., Bihrlé, A., Sabo, H., 1993. Dissociation between language and cognitive functions in Williams syndrome. In: Bishop, D., Mogford, K. (Eds.), *Language Development in Exceptional Circumstances*, Lawrence Erlbaum Associates, Hove, UK, pp. 177-189.
- Bickerton, D., Szathmáry, E. (Eds.), 2009. *Biological Foundations and Origin of Syntax*. MIT Press, Cambridge, MA.
- Bonabeau, E., 2002. Agent-based modeling: Methods and techniques for simulating human system. *Proceedings of the National Academy of Sciences of USA* 99(suppl. 3), 7280-7287.
- Boeckx, C., 2006. *Linguistic Minimalism: Origins, Concepts, Methods, and Aims*. Oxford University Press, Oxford.
- Boë, L-J., Heim, J-L., Honda, K., Maeda, S., 2002. The potential Neandertal vowel space was as large as that of modern humans. *Journal of Phonetics* 30(3), 465-484.

- Boë, L.-J., Heim, J.-L., Honda, K., Maeda, S., Badin, P., Abry, C., 2007. Acoustic capabilities and consequences for the debate on the origin of language. A reply to Lieberman (2007a). *Journal of Phonetics* 35(4), 564-581.
- Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., 1997. A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* 5(1), 49-62.
- Briscoe, T. (Ed.), 2002. *Linguistic Evolution through Language Acquisition: Formal and Computational Models*. Cambridge University Press, Cambridge.
- Brock, J., 2007. Language abilities in Williams syndrome: A critical review. *Development and Psychopathology* 19(1), 97-127.
- Bunge, S.A., Klingberg, T., Jacobsen, R.B., Gabrieli, J.D.E., 2000. A resource model of the neural basis of executive working memory. *Proceedings of the National Academy of Sciences of USA* 97(7), 3573-3578.
- Cangelosi, A., Parisi, D. (Eds.), 2002. *Simulating the Evolution of Language*. Springer, London.
- Cangelosi, A., Smith, A.D.M., Smith, K. (Eds.), 2006. *The Evolution of Language: Proceedings of the 6th International Conference*. World Scientific Press, Singapore.
- Cartling, B., 2008. On the implicit acquisition of a context-free grammar by a simple recurrent neural network. *Neurocomputing* 71(7-9), 1527-1537.
- Chomsky, N., 1986. *Knowledge of Language: Its Nature, Origin and Use*. Praeger, New York.
- Christiansen, M.H., Kirby, S., 2003a. Language evolution: Consensus and controversies. *Trends in Cognitive Sciences* 7(7), 300-307.
- Christiansen, M.H., Kirby, S. (Eds.), 2003b. *Language Evolution*. Oxford University Press, Oxford.
- Christiansen, M.H., Chater, N. (Eds.), 2001. *Connectionist Psycholinguistics*. Ablex Pub., Westport, CT.
- Clark, A., Lappin, S., 2011. *Linguistic Nativism and the Poverty of the Stimulus*. Wiley-Blackwell, Malden, MA.
- Clark, E.V., 2003. *First Language Acquisition*. Cambridge University Press, Cambridge.

- Clay, Z., Zuberbühler, K., 2009. Food-associated calling sequences in bonobos. *Animal Behavior* 77(6), 1387-1396.
- Cook, R.S., Kay, P., Regier, T., 2005. The world color survey database: History and use. In: Cohen, H., Lefebvre, C. (Eds.), *Handbook of Categorization in Cognitive Science*. Elsevier, Amsterdam, pp. 224-242.
- Corballis, M.C., 2002. *From Hand to Mouth: The Origins of Language*. Princeton University Press, Princeton, NJ.
- Corballis, M.C., 2007. Recursion, language, and starlings. *Cognitive Science* 31(4), 697-704.
- Coupé, C., Hombert, J.-M., 2002. Language at 70,000 BP: Evidence from sea-crossings. In *The Evolution of Language: Proceedings of the 4th International Conference Harvard*, pp. 27.
- D'Errico, F., Henshilwood, C., Nilssen, P., 2001. An engraved bone fragment from c. 70,000-year-old Middle Stone Age levels at Blombos Cave, South Africa: Implications for the origin of symbolism and language. *Antiquity* 75(288), 309-318.
- Deacon, T.W., 1997. *The Symbolic Species: The Co-evolution of Language and the Brain*. W. W. Norton, New York.
- Dryer, M.S., Haspelmath, M. (Eds.), 2011. *The World Atlas of Language Structures Online*. Max Planck Digital Library, Munich. Available online at <http://wals.info/>.
- Elman, J.L., 1990. Finding structure in time. *Cognitive Science* 14(2), 179-211.
- Elman, J.L., 2005. Connectionist models of cognitive development: Where next? *Trends in Cognitive Sciences* 9(3), 111-117.
- Enard, W., Przeworski, M., Fisher, S.E., Lai, C.S.L., Wiebe, V., Kitano, T., Monaco, A.P., Pääbo, S., 2002. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* 418, 869-872.
- Enard, W., Gehre, S., Hammerschmidt, K., Hölter, S.M., Blass, T., Somel, M., et al. 2010. A humanized version of Foxp2 affects cortico-basal ganglia circuits in mice. *Cell* 137(5), 961-971.

- Evans, N., Levinson, S.C., 2009. The myth of language universals: Language diversity and its importance for cognitive science. *Behavioral and Brain Sciences* 32(5), 429-492.
- Fadiga, L., Craighero, L., D'Ausilio, A., 2009. Broca's area in language, action, and music. *Annals of the New York Academy of Sciences* 1169, 448-458.
- Fedorenko, E., Behr, M.K., Kanwisher, N., 2011. Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences of USA* 108(39), 16428-16433.
- Felsenstein, J., 2004. *Inferring Phylogenies*. Sinauer Associates, Sunderland, MA.
- Fisher, S.E., Vargha-Khadem, F., Watkins, K.E., Monaco, A.P., Pembrey, M.E., 1998. Localization of a gene implicated in a severe speech and language disorder. *Nature Genetics* 18, 168-170.
- Fisher, S.E., Marcus, G.F., 2006. The eloquent ape: genes, brains and the evolution of language. *Nature Reviews Genetics* 7, 9-20.
- Fitch, W.T., 2010. *The Evolution of Language*. Cambridge University Press, Cambridge.
- Frederici, A., 2002. Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences* 6(2), 78-84
- Galantucci, B., 2005. An experimental study of the emergence of human communication systems. *Cognitive Science* 29(5), 737-767.
- Galán, J.M., Izquierdo, L.R., Izquierdo, S.S., Santos, S.I., del Olmo, R., López-Paredes, A., Edmonds, B., 2009. Errors and artefacts in agent-based modeling. *Journal of Artificial Societies and Social Simulation* 12(1). Available at: <http://jasss.soc.surrey.ac.uk/12/1/1.html>.
- Gentner, T.Q., Fenn, K.M., Margoliash, D., Nusbaum, H.C., 2006. Recursive syntactic pattern learning by songbirds. *Nature* 440, 1204-1207.
- Gong, T. 2009. *Computational Simulation in Evolutionary Linguistics: A Study on Language Emergence*. Institute of Linguistics, Academia Sinica, Taipei, Taiwan.
- Gong, T., Yang, R., Zhang, C., Ansaldo, U., 2010. Review of the summer institute in cognitive sciences 2010: The origins of language. *Biolinguistics* 4(4), 385-402.

- Gong, T., Shuai, L., Tamariz, M., Jäger, G., 2012. Studying language change using Price equation and Pólya-urn dynamics. *PLoS ONE* 7(3), e33171.
- Grainger, J., Dufau, S., Montant, M., Ziegler, J.C., Fagot, J., 2012. Orthographic processing in baboons (*Papio papio*). *Science* 336, 245-248.
- Grodzinsky, Y., Santi, A. 2008. The battle for Broca's region. *Trends in Cognitive Sciences* 12(12), 474-480.
- Groszer, M., Keays, D.A., Deacon, R.M.J., de Bono, J.R., Prasad-Mulcare, S., Gaub, S., et al. 2008. Impaired synaptic plasticity and motor learning in mice with a point mutation implicated in human speech deficits. *Current Biology* 18(5), 354-362.
- Hagoort, P., Brown, C.M., Groothusen, J., 1993. The syntactic positive shift (SPS) as an ERP measure of syntactic processing. *Language and Cognitive Processes* 8(4), 439-483.
- Harnad, S.R., Steklis, H.D., Lancaster, J. (Eds.), 1976. *Origins and Evolution of Language and Speech*. New York Academy of Sciences, New York.
- Harris, T., Wexler, K., Holcomb, P., 2000. An ERP investigation of binding and coreference. *Brain and Language* 75(3), 313-346.
- Hauser, M.D., 2010. The origin of the mind. *Scientific American* 301, 46-51.
- Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298, 1569-1579.
- Hauser, M.D., Barner, D., O'Donnell, T., 2007. Evolutionary linguistics: A new look at an old landscape. *Language Learning and Development* 3(2), 101-132.
- Huang, C-R., Lenders, W. (Eds.), 2004. *Computational Linguistics and Beyond: Perspectives at the Beginning of the 21th Century*. Institute of Linguistics, Academia Sinica, Taipei.
- Hurford, J.R., 2007. *The Origins of Meaning*. Oxford University Press, Oxford.
- Hurford, J.R., 2012. *The Origins of Grammar*. Oxford University Press, Oxford.
- Hurford, J.R., Studdert-Kennedy, M., Knight, C. (Eds.), 1998. *Approaches to the Evolution of Language: Social and Cognitive Bases*. Cambridge University Press, Cambridge.

- Hurst, J.A., Baraitser, M., Auger, E., Graham, F., Norell, S., 1990. An extended family with a dominantly inherited speech disorder. *Developmental Medicine and Child Neurology* 32(4), 352-355.
- Huson, D.H., Rupp, R., Scornavacca, C., 2011. *Phylogenetic Networks: Concepts, Algorithms and Applications*. Cambridge University Press, Cambridge.
- Jackendoff, R., 2002. *Foundations of Language: Brain, Meaning, Grammar, Evolution*. Oxford University Press, Oxford.
- Jackendoff, R., 2009. Your theory of language evolution depends on your theory of language. In: Larson, R.K., Déprez, V., Yamakido, H. (Eds.), *The Evolution of Human Language: Bilingual Perspectives*. Cambridge University Press, Cambridge (eds.), pp. 63–72.
- Jackendoff, R., Pinker, S., 2005. The nature of the language faculty and its implications for evolution of language (reply to Fitch, Hauser, and Chomsky). *Cognition* 97(2), 211-225.
- Ke, J., Holland, J.H., 2006. Language origin from an emergentist perspective. *Applied Linguistics* 27(4), 691-716.
- Ke, J., Minett, J.W., Au, C-P., Wang, W.S-Y., 2002. Self-organization and selection in the emergence of vocabulary. *Complexity* 7(3), 41-54.
- Kenneally, C., 2007. *The First Word: The Search for the Origins of Language*. Viking, New York.
- Kirby, S., 1999. *Function, Selection and Innateness: The Emergence of Language Universals*. Oxford University Press, New York.
- Kirby, S., Cornish, H., Smith, K., 2008. Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences of USA* 105(31), 10681-10686.
- Kong, L., Zhang, J.X., Kang, C., Du, Y., Zhang, B., Wang, S., 2010. P200 and phonological processing in Chinese word recognition. *Neuroscience Letters*, 473(1), 37-41.
- Kuhl, P.K., Rivera-Gaxiola, M., 2008. Neural substrates of language acquisition. *Annual Review of Neuroscience* 31, 511-534.

- Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: brain potentials reflect semantic incongruity. *Science* 207, 203-205.
- Kutas, M., Schmitt, B.M. 2003. Language in microvolts. In: Banich, M.T., Mack, M. (Eds.), *Mind, Brain, and Language: Multidisciplinary Perspectives*. Lawrence Erlbaum Associates, Mahwah, NJ, pp. 171-209.
- Lai, C.S.L., Fisher, S., Hurst, J.A., Vargha-Khadem, F., Monaco, A.P., 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413, 519-523.
- Larson, R.K., Déprez, V., Yamakido, H. (Eds.), 2009. *The Evolution of Human Language: Bilingual Perspectives*. Cambridge University Press, Cambridge.
- Lewis, M.P. (Ed.), 2009. *Ethnologue: Languages of the World*, 16th edition. SIL International, Dallas, TX. Online version: <http://www.ethnologue.com/>.
- Levinson, S.C., Gray, R.D., 2012. Tools from evolutionary biology shed new light on the diversification of languages. *Trends in Cognitive Sciences* 16(3), 167-173.
- Lieberman, P., Crelin, E.S., 1971. On the speech of Neanderthal man. *Linguistic Inquiry* 2(2), 203-222.
- Logothetis, N.K., 2008. What we can do and what we cannot do with fMRI. *Nature* 453, 869-868.
- Loreto, V., Steels, L., 2007. Social dynamics: Emergence of language. *Nature Physics* 3, 758-760.
- Luck, S.J., 2005. *An Introduction to the Event-Related Potential Technique*. MIT Press, Cambridge, MA.
- Lyon, C., Nehaniv, C.L., Cangelosi, A. (Eds.), 2007. *Emergence of Communication and Language*. Springer, London.
- MacWhinney, B. (Ed.), 1999. *Emergence of Language*. Lawrence Erlbaum Associates, Mahwah, NJ.
- Maess, B., Koelsch, S., Gunter, T.C., Friederici, A.D., 2001. Musical syntax is processed in Broca's area: an MEG study. *Nature Neuroscience* 4, 540-545.

- Marcus, G.F., 1999. Poverty of the stimulus arguments. In: Wilson, R.A., Keil, F. (Eds.), *The MIT Encyclopedia of the Cognitive Sciences*. MIT Press, Cambridge, MA, pp. 660-661.
- Mareschal, D., Thomas, M.S.C., 2006. How computational models help explain the origins of reasoning. *IEEE Computational Intelligence Magazine* 1(3), 32-40.
- Minett, J.W., Wang, W.S-Y. (Eds.), 2005. *Language Acquisition, Change and Emergence: Essays in Evolutionary Linguistics*. City University of Hong Kong Press, Hong Kong.
- Minett, J.W., Wang, W.S-Y. (Eds.), 2008. *Language, Evolution and the Brain*. City University of Hong Kong Press, Hong Kong.
- Minett, J.W., Wang, W.S-Y., 2008. Modeling endangered languages: The effects of bilingualism and social structure. *Lingua* 118(1), 19-45.
- Normile, D., 2012. Evolution of language: Experiments probe language origins and development. *Science* 336, 408-411.
- Oller, D.K., Griebel, U. (Eds.), 2004. *Evolution of Communication Systems: A Comparative Approach*. MIT Press, Cambridge, MA.
- Ouattara, K., Zuberbühler, K., N'goran, E.K., Gombert, J-E., Lemasson, A., 2009. The alarm call system of female Campbell's monkeys. *Animal Behavior* 78(1), 35-44.
- Oudeyer, P-Y., 2006. *Self-Organization in the Evolution of Speech* (translated by Hurford, J.R.). Oxford University Press, Oxford.
- Parisi, D., Mirolli, M., 2007. The emergence of language: How to simulate it. In: Lyon, C., Nehaniv, C.L., Cangelosi, A. (Eds.), *Emergence of Communication and Language*. Springer, London, pp. 269-285.
- Pepperberg, I.M., 1999. *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots*. Harvard University Press, Cambridge, MA.
- Piazza, M., Mechelli, A., Price, C.J., Butterworth, B., 2006. Exact and approximate judgments of visual and auditory numerosity: An fMRI study. *Brain Research* 1106(1), 177-188.

- Pinker, S., Bloom, P., 1990. Natural language and natural selection. *Behavioral and Brain Sciences* 13(4), 707-784.
- Poliak, S., Peks, E., 2003. The local differentiation of myelinated axons at nodes of Ranvier. *Nature Reviews Neuroscience* 4, 968-980.
- Price, G.R., 1970. Selection and covariance. *Nature* 227, 520-521.
- Pulvermüller, F., 2006. Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Academy of Sciences of USA* 103(20), 7865-7870.
- Reali, F., Christiansen, M.H., 2005. Uncovering the richness of the stimulus: Structure dependence and indirect statistical evidence. *Cognitive Science* 29(6), 1007-1028.
- Reinhart, T., Reuland, E., 1993. Reflexivity. *Linguistic Inquiry* 24(4), 657-720.
- Savage-Rumbaugh, S., Shanker, S.G., Taylor, T.J., 1998. *Apes, Language, and the Human Mind*. Oxford University Press, New York.
- Saxe, R., Brett, M., Kanwisher, N., 2006. Divide and conquer: A defense of functional localizers. *Neuroimage* 30(4), 1088-1096.
- Schalkoff, R.J., 1997. *Artificial Neural Networks*. McGraw-Hill, New York.
- Schoenemann, P.T., 2006. Evolution of the size and functional areas of the human brain. *Annual Review of Anthropology* 35, 379-406.
- Scott-Phillips, T.C., Kirby, S., 2010. Language evolution in the laboratory. *Trends in Cognitive Sciences* 14(9), 411-417.
- Scott-Phillips, T., Kirby, S., Ritchie, G. R. S., 2009. Signaling signalhood and the emergence of communication. *Cognition* 113(2), 226-233.
- Scott-Phillips, T., Tamariz, M., Cartmill, E.A., Hurford, J.A. (Eds.), 2012. *The Evolution of Language: Proceedings of the 9th International Conference*. World Scientific Press, Singapore.
- Shen, Z-W., 1997. Exploring the Dynamic Aspect of Sound Change. *Journal of Chinese Linguistics Monograph*, 11. University of California, Berkeley.

- Smith, A.D.M., Smith, K., Ferrer-i-Cancho, R. (Eds.), 2008. *The Evolution of Language: Proceedings of the 7th International Conference*. World Scientific Press, Singapore.
- Smith, A.D.M., Schouwstra, M., de Boer, B., Smith, K. (Eds.), 2010. *The Evolution of Language: Proceedings of the 8th International Conference*. World Scientific Press, Singapore.
- Smith, T.M., Toussaint, M., Reid, D.J., Olejniczak, A.J., Hublin, J-J., 2007. Rapid dental development in a Middle Paleo-lithic Belgian Neanderthal. *Proceedings of the National Academy of Sciences of USA* 104(51), 20220-20225.
- Sporns, O., 2011. *Networks of the Brain*. MIT Press, Cambridge, MA.
- Stam, J.H., 1976. *Inquiries into the Origin of Language: The Fate of a Question*. Harper & Row, New York.
- Steels, L., 2005. The emergence and evolution of linguistic structure: From lexical to grammatical communication systems. *Connection Science* 17, 213-230.
- Steels, L., 2009. Cognition and social dynamics play a major role in the formation of grammar. In: Bickerton, D., Szathmáry, E. (Eds.), *Biological Foundations and Origin of Syntax*. MIT Press, Cambridge, MA, pp. 345-368.
- Steels, L., 2011. Modeling the cultural evolution of language. *Physics of Life Reviews* 8(4), 339-356.
- Stout, D., Chaminade, T. 2012. Stone tools, language and the brain in human evolution. *Philosophical Transactions of the Royal Society B*. 367, 75-87.
- Stromswold, K., 2009. Genetics and the evolution of language: What genetic studies reveal about the evolution of language. In: Larson, R.K., Déprez, V., Yamakido, H. (Eds.), *The Evolution of Human Language: Biolinguistic Perspective*. Cambridge University Press, Cambridge, pp. 176-190.
- Tallerman, M. (Ed.), 2005. *Language Origins: Perspectives on Evolution*. Oxford University Press, Oxford.

- Tallerman, M., Gibson, K.R. (Eds.), 2012. *The Oxford Handbook of Language Evolution*. Oxford University Press, Oxford.
- Tomasello, M., 2008. *Origins of Human Communication*. MIT Press, Harvard.
- Van Heijningen, C.A.A., de Visser, J., Zuidema, W., ten Cate, C., 2009. Simple rules can explain discrimination of putative recursive syntactic structures by a songbird species. *Proceedings of the National Academy of Sciences of USA* 106: 20538-20543.
- Vargha-Khadem, F., Watkins, K.E., Alcock, K., Fletcher, P., Passingham, R., 1995. Praxic and nonverbal cognitive deficits in a large family with a genetically transmitted speech and language disorder. *Proceedings of the National Academy of Sciences of USA* 92(3), 930-933.
- Wang, C.C., Ding, Q.L., Tao, H., Li, H., 2012. Comment on “Phonemic diversity supports a serial founder effect model of language expansion from Africa”. *Science* 335, 657-c.
- Wang, W.S-Y., 1969. Competing changes as a cause of residue. *Language* 45(1), 9-25.
- Wang, W.S-Y., 1982. Explorations in language evolution. Reprinted in: Wang, W.S-Y. (eds.), *Explorations in Language*. Pyramid Press, Seattle, CA, 1991, pp. 105-131.
- Wang, W.S-Y., Ke, J-Y., Minett, J.W., 2004. Computational studies of language evolution. In: Huang, C.R., Lenders, W. (eds.), *Computational linguistics and beyond: Perspectives at the beginning of the 21th century*. Institute of Linguistics, Academia Sinica, Taipei, pp. 65-104.
- Wang, W.S-Y., Minett, J.W., 2005. The invasion of language: emergence, change, and death. *Trends in Ecology and Evolution* 20(5), 263-269.
- Watkins, K.E., Dronkers, N.F., Vargha-Khadem, F., 2002. Behavioral analysis of an inherited speech and language disorder: Comparison with acquired aphasia. *Brain* 125(3), 452-464.
- Wray, A. (Ed.), 2002. *The Transition to Language*. Oxford University Press, Oxford.
- White, S.A., Fisher, S.E., Geschwind, D.H., Scharff, C., Holy, T.E., 2006. Singing mice, songbirds, and more: Models for FOXP2 function and dysfunction in human speech and language. *Journal of Neuroscience* 26(41), 10376-10379.