

The evolution of language: a comparative review

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Abstract. For many years the evolution of language has been seen as a disreputable topic, mired in fanciful “just so stories” about language origins. However, in the last decade a new synthesis of modern linguistics, cognitive neuroscience and neo-Darwinian evolutionary theory has begun to make important contributions to our understanding of the biology and evolution of language. I review some of this recent progress, focusing on the value of the comparative method, which uses data from animal species to draw inferences about language evolution. Discussing speech first, I show how data concerning a wide variety of species, from monkeys to birds, can increase our understanding of the anatomical and neural mechanisms underlying human spoken language, and how bird and whale song provide insights into the ultimate evolutionary function of language. I discuss the “descended larynx” of humans, a peculiar adaptation for speech that has received much attention in the past, which despite earlier claims is not uniquely human. Then I will turn to the neural mechanisms underlying spoken language, pointing out the difficulties animals apparently experience in perceiving hierarchical structure in sounds, and stressing the importance of vocal imitation in the evolution of a spoken language. Turning to ultimate function, I suggest that communication among kin (especially between parents and offspring) played a crucial but neglected role in driving language evolution. Finally, I briefly discuss phylogeny, discussing hypotheses that offer plausible routes to human language from a non-linguistic chimp-like ancestor. I conclude that comparative data from living animals will be key to developing a richer, more interdisciplinary understanding of our most distinctively human trait: language.

Introduction

The evolution of human language is one of the most important and interesting evolutionary events in the history of life on our planet (Maynard Smith and Szathmáry 1995; Nowak et al. 2002). Nonetheless, the study of language evolution is often considered little more than speculative story-telling, and has played little part in the development of the many fields that touch upon it, including linguistics, evolutionary biology and neuroscience. However, since the early 1990s there has been increasingly productive study of language evolution from many different quarters, and a heartening increase in interdisciplinary collaboration and exchange. After decades of neglecting language evolution, linguists are turning to the topic with increasing interest, and evolutionary biologists are recognizing and grappling with problems language poses for evolutionary theory. There is an exciting new influx of relevant data from comparative biology and ethology, from molecular biology, from

neuroscience, and from mathematical and computational models of language evolution. There is increasing consensus about what the core problems are, and what types of data and theory will be relevant to solving them. Thus many empirical and theoretical strands are coming together in a nascent discipline, sometimes called ‘biolinguistics’ (Jenkins 1999), and the scientific study of language evolution seems to be coming of age.

In this review, I will start by identifying three components of the human language faculty that current consensus identifies as crucial: speech (signal), syntax (structure) and semantics (meaning). Then, I will discuss the evolution of various mechanisms underlying these component from a comparative viewpoint, highlighting new data from animal studies, molecular genetics, and computational modeling. Then I review some of the functional forces that may have played a key role during language evolution. Finally, I briefly review several phylogenetic hypotheses about the evolution of language. My intent in this review is to offer an entrée into this rapidly-growing literature, rather than an exhaustive review, and I emphasize newer data and cite up-to-date reviews wherever available. I recommend the essays in Christiansen and Kirby (2003) as an introduction to the ideas of many prominent contemporary theorists.

Three key innovations to be explained in language evolution

As recently stressed Hauser et al. (2002a), it is unproductive to discuss ‘language as an unanalyzed whole. Thus a critical first step in analyzing language evolution is to distinguish among its various component abilities. Most generally, any mechanism involved in language is part of the faculty of language in a broad sense (FLB). Mechanisms that are both specific to language and uniquely human can be termed the faculty of language in a narrow sense (FLN), which is a subset of the FLB. The contents of the FLN must be determined empirically rather than *a priori* (Hauser et al. 2002a). The purpose of delineating unique or unusual abilities is to help focus on the key innovations that occurred during human evolution, thus clarifying the problem, and not to draw lines in the sand dividing our species from all others (e.g. to provide a modern substitute for the soul). Indeed, traits that distinguish us from other primates but are shared with more distant species are of great interest, because these open the door to wider comparative study. Various mechanisms underlying speech, syntax or semantics have been proposed by different scholars as being both unusual in our species and crucial for language. Most scholars agree on the core importance of at least three of these: speech, syntax and semantics (Christiansen and Kirby 2003). Each component could, in principle, have a distinct evolutionary history, and require different explanatory principles.

Speech provides the standard signaling modality for the communication of language in all world cultures. Despite its reliance on an auditory and vocal apparatus that is broadly shared among most mammals, speech includes at least two components which are unusual, namely our reconfigured vocal tract

and vocal imitation. These components are crucial in understanding the evolution of our species' particular capacity for spoken language (as well as singing). However, the existence of signed languages among the deaf, and communication via writing, show that language can be conveyed by non-verbal means. Speech is important as the default signal, particularly because our primate relatives are unable to produce it, but should not be conflated with two other key components of language.

Syntax or 'grammar' is the generative system which allows the parsing and production of hierarchical structures in language; I will follow modern linguists by using this term broadly to denote not only sentence structure, but also some important structural aspects of phonology, morphology and semantics. The combinatorial power provided by the rules of language allows us to efficiently generate an unlimited set of distinguishable utterances from a limited set of meaningless phonetic units ('infinite use of finite means'). This is clearly a prerequisite for a system that can encode an unlimited set of concepts. Although syntax is apparently unique among living things, some of its structural aspects (particularly in phonology) appear analogous to those of music (another complex universal human behavior), and perhaps to music-like vocalizations among animals (e.g. bird or whale 'song') or even motor activities (e.g. Colonnese et al. 1996). Two aspects of human syntax that seem to be unique involve recursion (where structures can be iteratively embedded in similar structures to generate progressively more complex structures, e.g. phrases within phrases), and those which interface with reference (e.g. anaphora).

Finally, the critical component of human language that distinguishes it from music is our ability to encode and intentionally communicate an unlimited set of distinct propositional meanings, which I will gloss as '**semantics**'. Animal communication systems exist which, like speech, generate highly complex learned vocalizations (e.g. birdsong). However, our ability to use such signals to convey an unlimited range of meanings, from concrete ('there's a leopard in the right cave, but fruit in the left one') to highly abstract ('John's refusal to acknowledge Jim's plea for help was unethical'), appears to be unique. While other animals communicate meaningfully (e.g. emotionally-charged threat calls or screams, externally-referential food calls or alarm calls, or the honeybee 'dance language' (Hauser 1996)), only humans can communicate virtually any concept that they can entertain. Chimpanzees can certainly know about leopards, fruit, caves and much more besides (Tomasello and Call 1997), but are unable to communicate this propositional knowledge to others. This asymmetry between what is known and what can be said is made even more striking by the fact that, perceptually, nonhuman primates appear quite skilled at inferring complex meanings from sound (Bergman et al. 2003), despite their limited productive ability to encode such meanings.

Although they obviously interact to form a working system, each of these three critical components of spoken language should be analyzed independently. More fine-grained breakdowns are also possible, where smaller components of the above three broad categories are analyzed separately, such as

displacement, duality of patterning or recursion (Hockett 1960; Hauser et al. 2002a; Bickerton 2003). These three are thus intended only as useful blanket terms to focus and clarify discussion: by 'speech' I do not mean to exclude sign or other signaling mediums, and by 'syntax' I explicitly include structural aspects of phonology or morphology. Part of the rationale for this particular breakdown is to ease comparison with different animal species and cognitive abilities: each of these subdivisions may profit by comparison with different animal capabilities. Indeed, isolating these factors as important in language evolution required comparative data: the uniqueness (or lack thereof) of rich semantics or vocal imitation logically required comparison with animals. Until recently it was quite conceivable that dolphins or songbirds could communicate arbitrary propositions, or that monkeys could imitate arbitrary sounds. Only concerted effort and detailed empirical work by ethologists and comparative psychologists has demonstrated the contrary. Thus comparative data must inevitably play a central role in any adequate discussion of language evolution.

The comparative approach

A theme throughout this review will be the importance of a broad comparative approach to the evolution of language, which involves integrating data from a wide range of living species (and fossil evidence when available) (Lieberman 1968; Marler 1970a; Nottebohm 1976; Kuhl 1989; Hauser 1996; Hauser et al. 2002a). The fact that language appears to be unique among animal communication systems in no way reduces the value of animal research in understanding it, for several reasons. First, we need to know what animals can and can't do in order to know what aspects of human language are unique (as is true for any aspect of human biology). Despite being a logical necessity, this point is frequently ignored. Second, when some key component of language appears to be shared with animals, it can be studied using empirical techniques that would otherwise be inapplicable. For example, vocal imitation is necessary for language, absent in nonhuman primates, but abundantly observed in songbirds. The avian song learning system has been studied using single unit neural recording, gene expression assays, and experiments raising songbirds in the absence of song input (Doupe and Kuhl 1999). Such empirical work allows a rich mechanistic understanding of vocal learning, and the striking conservatism of vertebrate genetics, developmental and neural systems makes discoveries in songbirds surprisingly relevant to mammals and humans (e.g. the discovery of adult neurogenesis in songbirds, spurred its rediscovery in rats, monkeys and finally humans (Nottebohm 1999)). Finally, prudent examination of the comparative data allows evolutionary inferences that would otherwise be pure guesswork, both about the abilities of extinct ancestors, and about the nature of selective forces driving the evolution of various components of the language faculty. A broad comparative framework thus offers significant

advantages over more traditional human- (or perhaps primate-) centered approaches.

The modern comparative approach starts with a phylogenetic tree that illustrates the evolutionary relationships among various groups of living and extinct organisms. Groups related by common ancestry constitute ‘clades’. Among vertebrates, some relevant clades include tetrapods (air-breathing vertebrates like frogs, birds, reptiles and mammals), mammals (hairy milk-producing tetrapods like bats, cows, dogs and humans), and primates (large-brained and usually social mammals including rhesus macaques, chimpanzees and humans). These groups are obviously nested: humans are tetrapods, mammals and primates simultaneously. Humans share lungs and larynx with other tetrapods, lactation and molars with other mammals, and color vision with (some) other primates. The comparative approach allows two types of inferences to be made for any clade. First, traits that are shared (perhaps in modified form) within a clade by virtue of common descent (homologous traits (Hall 1994)) support inferences about extinct ancestors: we know that the ancestral mammal nursed its young with milk because all living mammals do so. Second, traits that have evolved independently in separate clades (analogous or convergent traits, a form of homoplasy) support inferences about selective forces (Gould 1976; Wake 1991; Sanderson and Hufford 1996). For example, sharks, ichthyosaurs and dolphins share their streamlined form because of parallel selection in each lineage for rapid controlled swimming under the constraints of hydrodynamics. The comparative approach thus supports inferences both about extinct ancestors (via homology), and about evolutionary constraints and selective forces (via analogy).

A key species in any comparative discussion of language evolution was the last common ancestor (LCA) of chimps and humans, which lived in Africa some 5–7 million years ago. We currently have no fossils of this species (hence it lacks any Latin name), and indeed our oldest undisputed fossils in the human line (small-brained bipedal hominids like *Australopithecus*) are only about half as ancient as the LCA (though see Brunet et al. 2005). It is important to note that the LCA was not a chimpanzee: chimpanzees have been independently evolving in the last 6 million years, and must differ in many respects from the LCA. Any complete theory of language evolution must take as its starting point the characteristics of the LCA (Seyfarth and Cheney, in press), which can be inferred using comparisons of humans with chimps and other great apes and primates.

Tinbergen’s four questions

From a biolinguistic perspective, Dobzhansky’s suggestion that ‘nothing in biology makes sense except in light of evolution’, applies with equal force to language. Evolution is multifaceted, and it is critical to distinguish several different levels of explanation and types of questions to be answered. Tinbergen (1963) distinguished four classes of biological questions, each of which is

equally important for complete understanding of the evolution of any trait. Mechanistic questions ('how is it implemented?') are often most empirically accessible: questions of speech production or neural processing of syntactic structures fall into this category. Developmental questions ('how does it develop ontogenetically?') delve further into how the mechanism comes into existence: child language acquisition is a vibrant empirical field investigating such questions with fascinating results (e.g. Locke 1993; Jusczyk 1997). Functional questions ('why did it benefit bearers over evolutionary time?') are the traditional province of modern behavioral ecology and sociobiology: questions concerning the selective benefit of vocal imitation or semantics are examples. Finally, phylogenetic questions ('how did the trait arise over evolutionary time?') require a reconstruction of the sequence of ancestral states of the mechanism in question, along with a plausible functional explanation of transitions between them. Gestural origins theories, or Darwin's theory of a musical 'protolanguage', are examples (Darwin 1871).

A general framework for understanding language evolution must attend to and explicate phenomena at all of these levels. Although our proximate level understanding of language mechanisms at the cognitive, neural and physiological levels is still incomplete, recent progress is rapid. Similarly, work on language ontogeny is rapidly providing insight into language acquisition and the neural mechanisms underlying it. Given the healthy momentum of empirical research on these proximate levels, it is the functional and phylogenetic questions that require most attention for researchers interested in language evolution. We require explicit hypotheses for the function(s) of language components, which are consistent with both the nature of language mechanisms and the timing of their development. And we need plausible phylogenetic paths from the LCA to modern humans that are consistent with current evolutionary theory, available comparative data, and the paleontological evidence. Successful models will ultimately integrate all four of Tinbergen's levels, along with additional, language-specific data such as the cultural phenomena of historical linguistics (Hurford 1990; Keller 1995; Deacon 1997).

An example: the comparative method and the descent of the larynx

Recent progress in understanding the evolution of speech provides a nice illustration of the value of the comparative approach (Lieberman 1968; Fitch 2000a, 2002). A key factor in human speech production is our unusual vocal tract: we have a descended larynx, hyoid and tongue root which enable us to produce a greater diversity of formant frequencies patterns, and thus of speech sounds, than would be possible otherwise. Such a descended larynx was believed until recently to be uniquely human, and thus has been emphasized in many accounts of language evolution (Lieberman 1984; Carstairs-McCarthy 1998). New comparative data call this emphasis into question. First, cinera-

diographic observations of nonhuman mammal vocalization indicate that mammals generally lower the larynx during vocalization, sometimes to a surprising degree (e.g. during dog barking). These observations suggest that lowering the larynx during vocalization is a primitive trait, shared among mammals (Fitch 2000b). Further, a number of species have now been discovered that possess a permanently descended larynx, including koalas, deer (Fitch and Reby 2001), and lions (Weissengruber et al. 2002). This is clearly an analogous trait, since the common mammalian ancestor of these species did not possess a permanently descended larynx. Since deer and lions do not use their descended larynx for speech, this repeated convergence indicates that some other selective force can drive the evolution of laryngeal descent. A likely candidate is selection to generate impressive vocalizations, which exaggerate the apparent size of the vocalizer by lowering formant frequencies (Ohala 1983; Fitch 1997; Maynard Smith and Harper 2003). This size exaggeration hypothesis applies not only to the nonhuman species with descended larynges (Reby and McComb 2003; Reby et al. 2005), but also accounts for the secondary human descent of the larynx seen only in males, and occurring at puberty (Fitch and Giedd 1999). Because the physical and physiological principles underlying this hypothesis apply equally well to humans, these findings demand caution when considering vocal tract reconfiguration during human evolution: selective forces other than speech might easily have driven laryngeal descent at one stage of our evolution, acting as a preadaptation for the phonetic capabilities exploited at some later stage.

These new data tell a cautionary tale: we must beware of considering any human trait unique without a thorough search among animals. More importantly they show the value of both homology and analogy in understanding the human capacity for speech. The discovery of laryngeal lowering during vocalization in many mammals suggests that this is a primitive trait, already present long before humans diverged from chimpanzees. The further discovery of a permanently descended larynx in several nonhuman species, which evolved convergently with that in humans, indicated that factors other than speech might select for such reconfiguration, and provided testable hypotheses for what these factors might have been. In sum, these data illustrate the value of the comparative approach to speech evolution, and suggest that the reconfiguration of the human vocal tract has been overemphasized in recent discussions of language evolution (e.g. Carstairs-McCarthy 1998).

Mechanisms underlying the three components: a comparative overview

With the value of a multifaceted Tinbergian approach, and a broadly comparative dataset, in mind, I now turn to a detailed consideration of the cognitive mechanisms underlying speech, syntax and semantics. A comparative consideration of the mechanisms underlying language allows us to isolate aspects of the FLB that are shared with other primates or mammals, along

with the 'key innovations' were necessary in to attain full natural language in the hominid lineage. Key innovations (Liem 1973) are traits that transform the selective pressures in an evolving lineage by allowing a new niche to be explored, or otherwise transform the selective regime acting on the lineage. Examples of key innovations in vertebrate evolution include lungs in tetrapods (allowing the conquest of land), feathers in birds (allowing flight), or milk production in mammals (allowing more effective maternal care). A number of key innovations may be tentatively identified *en route* to human language.

Speech and vocal imitation

In addition to the reconfiguration of the vocal tract, a second crucial component of the human speech capacity remains poorly understood: our highly-developed capacity for complex vocal imitation (Studdert-Kennedy 1983; Fitch 2000a). Imitation is a prerequisite for linguistic communication: without the ability to generate and acquire a large, open-ended vocabulary, the flexible, expressive power of language would be vastly reduced. Vocal imitative ability (an advanced form of vocal learning) has an unusual distribution pattern indicating multiple convergent evolution (Nottebohm 1976). Nonhuman primates are highly constrained in this respect, but birds, seals, bats and cetaceans readily learn to imitate vocalizations (Janik and Slater 1997). While apes can easily learn to recognize 100s of words (Savage-Rumbaugh et al. 1993), they cannot easily learn to produce any of them. Despite a common misconception, the primary limitation is at a neural and not a peripheral anatomical level: the basic vocal tract anatomy of a chimp or monkey, or even a dog or goat, would clearly support many of the phonetic contrasts found in human languages, if a human brain were in control (Lieberman 1968; Fitch 2000b). Vocal imitation evidently requires neural abilities not available in nonhuman primates, such as detailed voluntary control over vocalization and an ability to link auditory input to corresponding motor outputs (Jürgens 1998). Whether vocal imitation is domain specific, or a special case of a more general imitative ability (Donald 1991; Moore 1992) remains debatable. What is clear is that complex, flexible semantic communication demands a comparably complex, flexible phonological system to generate the signals, and such a phonological system is not available to our closest relatives, the chimpanzees, or to any other known nonhuman primate.

The convergent evolution of vocal imitation in a diverse set of species provides an excellent opportunity to understand the selective forces and constraints underlying the evolution of this trait (Marler 1970b). By far the largest and best-studied group of vocal imitators are the 4000+ species of songbirds (oscine members of the order Passeriformes), followed by parrots (Psittacidae) and some hummingbirds (Trochilidae). It is widely agreed that vocal imitation in these groups supports the development of a complex vocal

repertoire, but the functions of such complexity vary among species (Catchpole and Slater 1995). In general, it is male songbirds who sing, and their songs function as reproductive displays, repelling other males and attracting females. In some species, more complex repertoires have been shown to be more effective in territorial defense, and more attractive to females, and complexity is typically assumed to have resulted from sexual selection. However, there are many bird species in which females also sing, either alone or in complex duets with males, so this generalization is not absolute (Langmore 1998; Riebel 2003). Similar considerations apply to those mammals that are sophisticated vocal imitators, namely cetaceans (dolphins and whales) and seals (Janik and Slater 1997). The songlike vocalizations of the large baleen whales (Mysticete cetaceans), such as humpback whales (Payne 2000), appear to be made exclusively by males in a mating context (and thus to function quite similarly to birdsong), but vocal imitation in toothed whales like dolphins (Odontocetes) is found in both sexes. In summary, although vocal imitation is male-biased, and appears to have a strong sexually-selected component in the majority of species, other functions like group cohesion or pair-bonding are also attested. This large comparative database provides a valuable (although often neglected) empirical resource for theorists interested in this aspect of language evolution.

Neural and perceptual data

Noninvasive brain imaging has led to an explosion of data concerning the neural mechanisms underlying human spoken language; I will not attempt to review these data here (for a brief discussion of mirror neurons see Section 4.2.2). A metaanalysis of brain imaging studies including language is given by Cabeza and Nyberg (2000), while a more specific review of neural mechanisms involved in vocal perception in humans and nonhuman primates can be found in Scott (2005). An exciting development is the application of noninvasive imaging to nonhuman primates (Ferris et al. 2001; Logothetis et al. 2001), these techniques are now being used to explore auditory perception (Gil-da-Costa et al. 2004). The neuroanatomical bases for vocal production and control are reviewed in Jürgens (1998). Lieberman (2000) reviews converging data indicating the importance of subcortical mechanisms in language processing, while Szathmáry (2001) provides a provocative overview of the evolution of brain mechanisms involved in language. Finally, MacNeilage (1998b) provides one of the few attempts to integrate neural data with comparative data on primate vocal communication in a Darwinian framework to address a fundamental phenomenon of phonology: the alternation of consonants and vowels.

In addition to the production mechanisms just discussed, certain components of the speech perception system are potentially unique. Speech researchers have traditionally posited that speech relies on perceptual mechanisms that are unique, both to our species and to speech itself (vs. music or other nonspeech sounds) (Lieberman et al. 1957; Lieberman and Mattingly 1985). This hypothesis is nicely summarized by the claim that ‘speech is special’

(Lieberman 1996). However, despite repeated suggestions along these lines (often made in the absence of relevant animal data, e.g. Sussman et al. 1998), many putatively 'special' aspects of speech perception now appear to be widely shared. Examples include categorical perception (Kuhl and Miller 1978) and the closely-related 'prototype magnet' effect (Kluender et al. 1998), vocal tract normalization (Fitch 1997), and discrimination among human languages by rhythmic cues (Ramus et al. 2000). Although many speech phenomena remain to be tested (e.g. duplex perception, trading relations and the McGurk effect (Lieberman and Blumstein 1988)), it currently seems prudent to assume that the perceptual mechanisms underlying speech are broadly shared, until convincing comparative evidence to the contrary has been presented. See Kuhl (1987), Doupe and Kuhl (1999), Sinnott and Williamson (1999) and Hauser (2001) for further discussion.

Molecular data: FOXP2 and the evolution of speech

Molecular genetics represents an area of great interest for understanding language evolution. Rapid progress in genetic sequencing technology has provided us with relatively exact determinations of the human, chimpanzee, rat, mouse and chicken genomes (along with many nonvertebrates); drafts of the macaque and dog genomes are nearing completion. These data allow us to isolate the small percentage of genes that differ between humans and other species. Because the fundamental capabilities underlying language appear to be identical among all populations of normal humans, we can exclude from consideration alleles that differ between human populations, thus isolating a candidate set of genes coding for the many biological differences between humans and chimpanzees. In addition to language, these include brain size, erect bipedalism, sexual function, and many others. Although this set of genes forms a tiny percentage of the total human genome (around 1.5%), it equates to a bewildering 30 million base pairs of DNA that could play a role in the genetics of human uniqueness. Because we have little detailed knowledge of what functions most of this DNA performs, we are still a long way away from isolating the genetic differences playing a crucial role in human language ability. Searching for language-related genes among the many candidates is still akin to searching for a needle in a haystack, and both intense research and good luck will be necessary for success in the short term.

Fortunately, a combination of hard work and luck has provided the first language-related gene that is both the same in all normal human populations and functionally different from that of chimpanzees. Called Forkhead-box P2, or FOXP2, this gene is a member of a large and ancient gene family that codes transcription factors (proteins that bind to DNA, thus regulating the expression of other genes). The gene was first identified clinically, by virtue of a deleterious mutation in a large British family, using a combination of traditional cognitive neuropsychology and Mendelian genetics (Vargha-Khadem et al. 1995). Affected members of the family have a number of difficulties, focused on problems with oro-motor praxis including speech production and

non-speech oral movements, and including some less distinct cognitive and perceptual deficits (Vargha-Khadem et al. 1998). Early reports that this mutation affected only morphological syntax (Gopnik 1990), leading to the misleading term 'grammar gene' (Pinker 1994), were based on little data and inadequate controls, and have been widely repudiated (Marcus and Fisher 2003). However, the correction of this misinterpretation in no way diminishes the importance of FOXP2, given the importance of increased oro-motor control in the evolution of spoken language. Studies of affected members using noninvasive brain imaging have already begun to uncover the anatomical (Belton et al. 2003) and physiological (Liégeois et al. 2003) underpinnings of the deficits caused by the mutated allele.

The isolation of the gene to a particular region of chromosome 7, aided by the fortuitous discovery of an unrelated individual with similar symptoms and a closely-related mutation, allowed researchers to finally isolate and sequence the FOXP2 gene (Lai et al. 2001). Shortly thereafter, researchers compared the DNA sequence of this gene in multiple human populations with that of the mouse and chimpanzee (and other apes) (Enard et al. 2002). The human version of the gene is functionally identical in all normal populations worldwide, but differs significantly from our nearest animal relatives, the chimpanzees. Of numerous minor changes at the level of individual base-pairs, only two changes lead to changes at the protein (amino acid) level. Statistical analysis of the pattern of changes gave a (relatively imprecise) estimate of when these changes occurred in human phylogeny, somewhere between 200,000 years ago and the present (Enard et al. 2002). Thus, a simple and relatively recent change of two amino acids in a protein is enough to result in major behavioral and cognitive changes in the human lineage. Work is currently in progress to genetically engineer a mouse with copies of the human gene. Although no one expects this will result in a talking mouse, it will enable a detailed investigation of the effects of the FOXP2 gene on mammalian neural development, and identification of the cascade of other genes that the FOXP2 transcription factor presumably regulates.

Thus, the isolation of the first gene that is both clearly linked to a high-level human function (spoken language) and is a derived trait in humans (differing from chimps and identical among human populations) is cause for considerable excitement. However, it is obvious that changes in many other genes were necessary for the shaping of the language faculty during human evolution, and at present we can only guess at how many there might be. If FOXP2 is any example, surprisingly small genotypic changes may lead to major changes at the phenotypic level, which could make the search for relevant genes quite difficult. The combination of luck and immense research effort that went into uncovering FOXP2 is also sobering: if there are 100 such genes we are a very long way off from isolating them all. However, a number of candidate genes can already be identified due to their involvement in various language disorders (Stromswold 2001). Another fascinating gene, involved in brain size regulation, is called ASPM (Evans et al. 2004); null mutations in humans lead to a 70%

decrease in brain volume. Although a direct link between brain size and language is questionable (several animal species, including dolphins, have larger brains than humans but lack language), the brain size increases that occurred during human phylogeny certainly constitute a crucial aspect of our biology. I conclude that comparative molecular genetics, combined with cognitive and neuroscientific investigations, offer great promise to ground discussions of language evolution at the level of specific changes in DNA during human evolution.

In summary, the combination of a well-established interdisciplinary field of speech science and a rich comparative database has provided a firm foundation for work on the evolution of speech, and new neural and molecular data have made this one of the most solid and exciting domains of research on the evolution of language. Although well-articulated integrations of this large database remain challenging (MacNeilage 1998b; Arbib 2003), this field has seen considerable progress. See Fitch (2000a, 2002) for further review.

Semantics: call production and perception in nonhumans

Considerable recent progress in the study of the semantic aspects of language evolution has come from comparative studies of animal communication and perception. Much early work in this field focused on attempts to teach language-like communication systems to animals, including apes, parrots and dolphins. Such comparative work has revealed a number of important facts. Briefly, attempts to teach apes language have clearly demonstrated that great apes have virtually no ability to imitate speech sounds, but can be trained to communicate via various manual means, developing a 'vocabulary' of more than 100 items. Further, bonobos, especially those exposed early in development to language usage and reinforcement, acquire a considerable facility for perceiving multiword spoken utterances, including some elements of basic syntax such as word order (Savage-Rumbaugh et al. 1993). Dogs can rapidly learn the meanings of many human words (Kaminski et al. 2004). Parrots, of course, readily learn to imitate speech, and with the proper socially-competitive training regimen, parrots can also link the sounds of many words to their real-world referents at an impressive level, belying the pejorative connotation of the verb 'to parrot' (Pepperberg 1991). Finally, dolphins also have well-developed imitative skills (Richards et al. 1984), and like parrots can be trained to use vocal signals referentially (Herman et al. 1993). There is no evidence for more complex aspects of syntax such as phrase structure, embedding, or long distance dependency in any of these species (Kako 1999). Despite the reliance of such studies on intensive training and feedback (far beyond what a normal human child needs to acquire language) these studies both demonstrate significant 'latent' communicative abilities in each of these species, and allow us to draw the inference that similar abilities were present in (at least) our LCA with chimps. The components of language competence *not* demonstrated by

language-trained animals are equally enlightening, revealing what needed to evolve in the hominid line *en route* to modern language (e.g. vocal imitation). Thus, empirical work on this topic is important and needs to be supported rather than dismissed (e.g. Wallman 1992; Pinker 1994), and the charged rhetoric surrounding such efforts is regrettable. For balanced reviews see Deacon (1997), Kako (1999).

Field studies of animal communication using new empirical techniques have played an important role in demonstrating similarities and differences between language and animal communication systems. It is now clear that many animals have 'functionally referential' alarm and food calls (Cheney and Seyfarth 1990b; Hauser et al. 1993; Hauser and Marler 1993; Evans et al. 1993). By this, ethologists mean that calls reliably provide listeners with information about external referents (such as eagles vs. leopards). There is also considerable evidence of 'audience effects', where a caller's behavior is affected by the presence or absence of conspecifics, in species from chickens to monkeys (Karakashian et al. 1988; Cheney and Seyfarth 1990b; Evans and Marler 1994). However, a variety of experiments strongly suggest that such calls are not *intentionally* referential on the part of signalers: callers do not appear to shape their calling in ways relevant to the knowledge (or lack thereof) of their listeners (Seyfarth and Cheney, in press). For example, vervets producing alarm calls continue to do so even after all group members have seen the predator and escaped to safety. More striking, a macaque mother who sees a predator (or food) hidden in a test chamber makes no alarm (or food) calls when her infant (who did not see the hidden stimulus) is released into the chamber (Cheney and Seyfarth 1990a). Apparently, monkeys' lack of a 'theory of mind' makes such intentionally communicative calling impossible for monkeys (Tomasello and Call 1997; Seyfarth and Cheney, in press). This, combined with the fact that alarm call production appears to be unlearned (and is thus strictly genetically limited in productivity), argues against the widespread presumption that alarm calling in monkeys represents a direct precursor of words in human language. Although there is still some controversy about theory of mind in apes (Povinelli and Eddy 1996; Tomasello et al. 2003), apes appear to lack 'functionally referential' calls. In any case, a few calls does not constitute a language, and there is no evidence for a rich propositional semantics in the natural communication system of any nonhuman species (Hauser 1996).

In sharp contrast to their rather limited abilities to convey information intentionally, experimental data reveal highly-sophisticated perceptual and interpretative abilities in nonhuman primates. Not only do monkeys react appropriately to their own conspecific alarm calls, but they learn to react appropriately to calls of other species as well (e.g. Seyfarth and Cheney 1990; Owren et al. 1993; Zuberbühler 2000b). Furthermore, they react appropriately to sequences of calls experimentally manipulated to 'stage' different types of social interactions, looking longer to simulations of an important dominance reversal than to simulations where the dominance hierarchy remains

unchanged (Bergman et al. 2003; Seyfarth et al. 2005). Such data clearly show that primates' perception of calls entails a complex inferential and interpretative system. Combined with other data revealing rich cognitive abilities in nonhuman primates, such data increasingly paint a picture of nonhuman primates as having quite complex minds, particularly in the social realm, but lacking a communicative mechanism capable of expressing most of this mental activity.

Syntax: phrase structure and emergent structure

Primates often emit sequences of calls, not just a single call (e.g. Fischer and Hammerschmidt 2002), and converging data indicates that sequential structure in these call bouts is identified and used by perceivers (Bergman et al. 2003; Seyfarth et al. 2005). There has been increasing recent interest in the sequencing and syntactic abilities of nonhuman primates. Recent laboratory work reveals a surprisingly sophisticated ability of macaques to memorize sequences, and to rapidly output (pressing a touch screen) sequences in the manual domain (Terrace et al. 2003). On the perceptual side, tamarins can identify rule-based sequences using transitional probabilities (Hauser et al. 2001; Hauser et al. 2002b; Fitch and Hauser 2004), without training. In the field, forest guenons are sensitive to the serial order of calls in a multi-call sequence (Zuberbühler 2000a, 2002). All of this work suggests that the traditional focus on semantic information at the single-call level (treating primate calls like words, (e.g. Carstairs-McCarthy 1999)) overlooks a considerable informational capacity potentially available in *sequences* of calls.

However, human syntax is not limited to sequential structure or transitional probabilities. A foundational insight of modern linguistics is that higher-order hierarchical structure is present and necessary in human languages (Chomsky 1957). In particular, the simplest form of generative rule system, called a finite-state grammar, which encodes sequential regularities in a signal, is inadequate to capture the structure of any human language. More powerful grammars, called phrase structure grammars, are required to capture the long-distance dependencies and phrasal nesting found in natural languages (or mathematical and computer programming expressions). The necessity for phrase structure in language is one of the few areas of apparently complete agreement among syntacticians of various theoretical backgrounds (Sampson 1980; Jackendoff 2002). Interestingly, despite the well-documented serial processing abilities of some nonhuman primates, recent data suggests that their ability to process phrase structure are limited (Fitch and Hauser 2004). Cotton-top tamarins exposed to nonsense speech strings composed according to a finite-state grammar easily mastered it, without training, as revealed by their ability to recognize novel strings composed by a different rule. However, they repeatedly failed to master a closely matched phrase structure grammar, although composed of the same speech syllables and tested with the same techniques.

Combined with studies demonstrating failure by monkeys at arbitrarily transposed melody perception (e.g. D'Amato 1988; Wright et al. 2000), these data suggest that something that comes very naturally to humans – perceiving phrase structure and relationships between distant items – may be difficult or impossible for other primates. If true, this would be an important constraint on language learning abilities in these animals, adding to the list of what needed to evolve in humans.

Mathematical and computational modeling: A-Lang research

Another area of considerable interest is the rapidly-expanding discipline of mathematical and computer modeling of language evolution. The last decade the field has witnessed an explosion of research in this vein, often termed 'artificial language' modeling or 'A-Lang' research. I will only indicate a few of the most interesting strands of this research (for more detail see Kirby 1998, 2002; Briscoe 2002; Komarova and Nowak 2003). A wide variety of approaches have been employed, from purely formal mathematical models (Nowak et al. 2001; Komarova and Nowak 2003) to detailed connectionist computer models (Batali 1998), in some cases including interactions among physical robots (Steels 1998, 1999). Much of the work in this field involves computer simulations of populations of simple 'agents' (Kirby 1998). More detailed models of gene/culture coevolution explore such issues as the evolution of Universal Grammar (Nowak et al. 2001), or the Baldwin effect and grammatical assimilation (Batali 1994; Briscoe 2003). This branch of evolutionary linguistics has produced converging results that are relevant to some of the central questions in language evolution, and that have long resisted resolution by more traditional empirical methods (for reviews see Steels 1997; Briscoe 2002; Cangelosi and Parisi 2002; Kirby 2002).

An important principle underlying much of the A-Lang work is that language involves cultural transmission between generations, which creates a novel level of change, slower than ontogenetic learning but much faster than phylogenetic change. This is because a given generation of learners receives as its input (the primary linguistic data from which they will induce a grammar) the output of other individuals, who were themselves once learners. Thus a complete picture of language evolution involves an intermediate level of analysis, between the two standard levels of ontogeny (neural development and acquisition by individuals) and phylogeny (gene changes in populations). This level has been aptly dubbed 'glossogeny' (Hurford 1990), and a key feature is that glossogenetic change is rapid compared to phylogenetic change. The existence of this additional level of cultural 'evolution' is to some extent a self-evident fact: languages change over historical time, and their rate of change is much faster than human genetic change (French and Spanish have become mutually unintelligible in less than 2000 years, despite little relevant genetic change between Romance-speaking populations). Historical linguistic change has been studied for centuries, and has certain parallels with biological evolution that were already noted by Darwin (1871). A formal framework for

characterizing this level of change is still under development (e.g. Lightfoot 2002; Kirby et al. 2004). It is clear however that language change inevitably results from a simple fact about language acquisition: language learners induce a grammar based on the output of past language learners, and because this output is limited and imperfect, the induced grammar will often be slightly different from that of the model, resulting in language change. Such change occurs in the absence of any biological change in the language acquisition system itself. Although such historical change may to some extent be random, akin to drift in population genetics, and some changes may make the system more functional (e.g. for more effective communication or thought), and thus akin to adaptation by natural selection, a third component will be 'adaptive' in a different (and non-biological) sense: the language will change to fit any biases intrinsic to the language acquisition system itself. Put another way, the primary linguistic data serving as input to generation x will be modified (and often streamlined) by any cognitive constraints, making the linguistic strings output by generation x (which serves as the primary linguistic data for generation $x + 1$) more learnable. This is true regardless of whether the cognitive constraints in question are specific to communication or to language: while functional pressures may clearly play a role, other more general processing constraints may be equally important (e.g. perceptual or memory constraints, ease of storage, access or productions, limits on complexity, etc).

This verbal argument (Darwin 1871; Deacon 1997) has been confirmed in a diverse array of modeling studies (summarized in Kirby 2002): communicative structure can emerge at this temporally intermediate 'glossogenetic' level. Starting with a 'seed' of completely random unstructured signals, a population can develop a highly-organized system through an iterative cultural transmission process distributed over space and time, without any 'biological' change in the makeup of the agents being required. Of particular interest is the emergence of vowel systems (de Boer 2001; Oudeyer 2003) and of grammatical regularities (Kirby 1998; Zuidema 2005) that often bear only an indirect relationship to constraints built in to the model. Relatively general constraints at the perceptual or cognitive level can lead to quite specific effects on the structure of the evolved communication systems in a short time period. This type of work offers a rather different perspective on questions of learnability that are at the heart of much theoretical debate in linguistics (Pinker 1984) and offers a way out of sterile 'nature vs. nurture' debates. While some see the rapid acquisition of language by children as evidence for innate knowledge (Crain 1991), and others see it as evidence of powerful learning mechanisms (Bates and Elman 1996), the recent modeling work makes explicit a middle road between these extremes. Innate constraints (on learning, storage, access, production or other aspects of linguistic performance, or specific to linguistic competence), when iterated over many generations, progressively filter even a completely random and hard-to-learn communicative system to make it progressively more learnable. This research confirms a core principle of nativist linguistics: that a biased or constrained learner will be superior to an unbiased

learner at picking up a culturally-transmitted signal system (Kirby et al. 2004). However, it also means that the biases do not have to be specific to the linguistic system, as is often assumed: any old bias will do, and the more biased, the smaller the potential search space of grammars (Nowak et al. 2002). Crucially, this result weakens the scope of the ‘argument from design’ in language evolution (Pinker and Jackendoff 2005): when biased glossogenetic change is possible, a close fit between language and learners does not necessarily indicate a phylogenetic adaptation to communication or language.

The necessity for populations in such modeling results sit well with the empirical observations of language development. A single child, alone, never creates a full, grammatically-structured language *de novo*. However, a group of children interacting socially *will* do so, as shown recently by the fascinating development of Nicaraguan Sign Language over a short period of time (Senghas and Coppola 2001; Senghas et al. 2005; Emmorey 2002). A certain critical mass of individuals, and the resultant distributed and iterated communicative process, appears necessary for this to occur. A second emerging result is that the number of utterances conveyed in a population, or between generations, plays a critical role in the behavior of the model: with small numbers of utterances no system emerges, and with huge numbers perfect learning occurs (and no glossogenetic change). The interesting phenomena emerge between these two extremes (Kirby 2002). In summary, mathematical computer modeling of language change constitutes a powerful new addition to the tools available for studying language evolution, and one of the most rapidly-growing subfields in the discipline. Unfortunately, this sub-field is currently rather fragmented: a number of schools have developed with little interaction or cross-pollination, whose practitioners rarely draw explicit comparisons between approaches and models, and with a proliferation of techniques and terminologies. Coherent progress in this rapidly growing field will require A-Lang researchers to overcome this isolationism, or risk being ignored by the rest of the field.

Summary: mechanisms and key innovations underlying language

As this overview shows, our understanding of the evolution of each of these three major novel components underlying language is rapidly increasing. Comparative data on nonhuman primate cognition and communication, as well as communication in other groups such as birds, have allowed us to focus on mechanisms that play a key role in language but appear to be lacking in our nearest living relatives, minimally including vocal learning, intentionally semantic vocal production, and phrase structure parsing. Exciting advances in molecular genetics have led to the discovery and sequencing of the first gene tied to language that differs between humans and chimps. Advances in the mathematical framework for describing language evolution, and converging evidence from computational simulations, have sharpened the focus on what

may or may not need to be genetically coded for children to acquire language, and the study of an intermediate glossogenetic level of change, between the phylogenetic and ontogenetic levels, offers a middle way out of unproductive nature versus nurture debates. The apparent inability of monkeys to represent others' minds may account for their inability to use calls in an intentionally informative manner. In short, considerable progress has been made recently in understanding the mechanisms underlying language from a comparative perspective, which shows no signs of slowing. With these insights concerning comparative data and proximate mechanisms in hand, I now turn to ultimate evolutionary questions about language, concerning function and phylogeny.

Ultimate function: types of selection underlying language evolution

Darwinian evolution by natural selection entails two independent components: a system for generating variation (including recombination and random genetic mutation) and a system that selects among these diverse variants. As recognized by Darwin, both components operate within a diverse set of constraints (including physical, developmental and historical constraints). While some progress has been made delineating evolutionary constraints on a morphological level (e.g. Goodwin and Trainor 1983; Maynard Smith et al. 1985), little is currently known about the role of such constraints in language evolution. Regarding the generation of variability, there is no reason to believe that language evolution requires anything more than the standard processes of recombination and mutation. However, regarding the selective component of evolution, there is more room for debate. Theorists often find it useful to distinguish between natural selection, sexual selection and kin selection. (Despite a recent revival of interest in 'group selection' it remains unclear that proposed terminological innovations have any practical significance beyond classical kin selection (Maynard Smith 1998; Sober and Wilson 1998)). Although there is nothing sacred about this three-way partition, a significant body of evolutionary theory suggests that these three subtypes of selection are profitably distinguished, because each entails different constraints and possibilities. Thus, for example, sexual selection entails the possibility of 'runaway selection' if heritable female preference for extreme male traits exists (Fisher 1930), while 'honesty' in such situations (the degree to which signals accurately convey information) is hard to evolve (Maynard Smith 1991; Maynard Smith and Harper 2003). By partitioning the selective variance underlying language evolution we can thus both clarify the questions, and potentially take advantage of existing theoretical work to generate testable predications.

In the context of language evolution, individually-focused **natural selection** (in the narrow sense) presumably underlies many of the basic cognitive components underlying the FLB (e.g. basic associative learning, memory, and complex conceptual abilities like discrimination, categorization, induction etc.) via natural selection on individual behavior during the evolution of the

vertebrate brain. It is less clear that natural selection alone can account for the more novel aspects of language like phonology or semantics. One possibility is that core aspects of language evolved initially to aid thought, and is thus primarily a cognitive adaptation, providing the bearer with a private conceptual system of great power for use both in environmental and social problem-solving. This idea neatly solves the perennial 'lone mutant' problem: who would the first language user talk to? (Answer: no one). However, this hypothesis can't account for vocal learning, or the meaning-to-sound mapping function of language (both of which seem superfluous to purely 'private' function). Nor is it clear that 'private language' (that is, linguistic thought) would be particularly useful without a rich culturally-conveyed set of words, socially accreted over generations in the lexicon. Another argument in support of the 'language for thought' hypothesis is the preponderance of private linguistic thought in our everyday lives. However, many biological systems are clearly 'intended' for functions that they rarely attain (e.g. sperm or seeds), sapping some of the force of this argument. Thus, despite the clear role of pure natural selection in shaping many or most of the conceptual capacities underlying language, and the undeniable fact that language is extremely useful in individual behavior (imagine Robinson Crusoe without language), most theorists have emphasized social selective forces in the evolution of other aspects of language.

Sexual selection, resulting from mating competition and female choice, has repeatedly been put forward as an important selective force in language evolution, since the concept was introduced by Darwin (1871). Its presumed importance is implied in the statement that 'subjacency has many virtues, but I am sure that it could not have increased the chances of having fruitful sex' (Lightfoot 1991, p. 69). 'That tribal chiefs are often both gifted orators and highly polygynous is a splendid prod to any imagination that cannot conceive of how linguistic skills could make a Darwinian difference' (Pinker and Bloom 1990, p. 725). Such statements, which could be multiplied considerably, seem to rest on an implicit assumption that complex language could increase mating success directly, by making the speaker attractive to potential mates. This idea, understandably popular among academics, appears to be taken for granted by an otherwise diverse group of authors (e.g. Pinker and Bloom 1990; Bickerton 1998; Dessalles 1998; Miller 2001). However, theoretical models of the evolution of communication indicate that assumptions of this sort are unjustified. A substantial theoretical literature makes clear that 'honest' communication of any sort is difficult to evolve, particularly in sexually selected systems (Fitch and Hauser 2002; Maynard Smith and Harper 2003). This is because the ubiquity of conflicting interests tends to either select for exaggeration in signalers (and in turn to perceivers ignoring their signals (Dawkins and Krebs 1978)) or to a few expensive, energetically wasteful displays with fixed meanings (Zahavi 1975; Grafen 1990). To evolve an open-ended communication system like language, that can be used to communicate flexibly and 'honestly',

the dual traps of Machiavellian deceit and wasteful Zahavian handicaps must be avoided (Fitch 2004).

The comparative data reviewed above provide an interesting perspective on the role of sexual selection in language evolution. If we look among animals for communication systems with vocal imitation and complex structure, we find that most of these systems are sexually-selected (bird and whale song are typically produced mainly by males and function as inter- or intra-sexual displays). Although complexity appears to be rewarded for its own sake in these systems, propositional meaning is apparently absent, and contemporary evolutionary theory makes clear why: in a sexually-selected system there is no benefit to a singing male to honestly convey propositions to other male competitors. Attempts to attract females by conveying information will always be bedeviled by the pressure on males to exaggerate, and consequent pressure on females to ignore any supposed content (and similarly with aggressive displays). These comparative data thus suggest that although sexual selection might have played a role in evolving vocal imitation and some structural precursors of syntax, we must look elsewhere to understand complex, 'honest' semantics. Of course, there is no doubt that language is *utilized* in human courtship (Miller 2001), but this is hardly surprising since language is integrated into virtually all human social behavior. It may also be true that men's use of language is often more ostentatious and aggressive than women's – potential signs of a sexually-selected trait (Locke and Bogin, in press). But this may stem from men being more competitive, in general, rather than from sexual selection on language in particular.

Furthermore, two key predictions for a sexually-selected system fail for language. First, sexually-selected systems in mammals typically result in hypertrophied versions of the selected trait in males. In contrast, language abilities are evenly distributed in humans, and if anything females have the upper hand (Hyde and Linn 1988; Henton 1992). Second, sexually-selected traits (in either sex) typically mature at puberty, when they become useful, and not before. But language abilities are remarkable precisely because they come online so early in human ontogeny: language learning actually begins before birth (DeCasper and Fifer 1980; Mehler et al. 1988), and after three years the linguistic abilities of human children have already surpassed adults of any other known species. This early ontogeny is also a difficulty faced by models of 'language for status' (e.g. Burling 1986; Dessalles 1998) – in both cases the ability in question (complex, honest communication) appears in individuals long before it is needed to serve the hypothesized function. In summary, it seems quite unlikely that sexual selection could drive those critical semantic components of language that underlie meaning.

Kin selection represents an appealing alternative to sexual selection as a key selective force in the evolution of language. While both natural and sexual selection were delineated by Darwin, the importance of kin selection was discovered much later by Hamilton (1964), and is the most significant recent addition to evolutionary theory. The core notion is 'inclusive fitness'. From a

gene's perspective the relevant evolutionary issue is not the survival of a particular individual body in which an allele finds itself, but of ALL the bodies in which that allele is present. Since the chance of two individuals sharing a rare allele will be directly proportional to their relatedness r , individuals who 'altruistically' share resources preferentially with kin may actually be acting in their own 'genetic best interests'. Besides its obvious applicability to parental care, Hamilton's insight provided a solution to a problem that had deeply troubled Darwin: the problem of cooperative Hymenopteran insects (ants, bees, and wasps) in which worker females do not reproduce themselves, but instead tend and protect the offspring of the queen bee. As Hamilton realized, the offspring are all sisters of the workers (who thus are looking after their own genes). A quirk of Hymenopteran biology is that sisters can actually be closely related to one another (and thus more likely to share genes) than they are to their own offspring (Wilson 1975). Thus from a kin selection viewpoint, the honeybee care system makes perfect sense. This is clearly equally true of the famous communication system of honeybees enabling their cooperative sharing of information. The evolution of signaling among relatives obeys quite different rules from those underlying non-kin communication, and honest, low-cost signals can evolve quite easily (Johnstone and Grafen 1992; Bergstrom and Lachmann 1998; Maynard Smith and Harper 2003). Thus, unlike sexually-selected systems, in the kin-selected honeybee 'dance language' (von Frisch 1967), there is less conflict of interest and thus much less selection for 'dishonest' communication among the sisters of the hive.

Turning back to language, kin selection offers an elegant solution to some of the problems discussed above (Fitch 2004). In sexual selection, conflicts of interest between communicators continually threaten to derail an evolving 'honest' communication system. In contrast, communicating kin often share each others' genetic best interests, so kin selection will favor an individual (especially a parent) who can increase a relative's (particularly, offspring) survival by communicating information about food or predators. There is no need for wasteful Zahavian handicaps, nor any intrinsic limit on the number or type of messages to be conveyed. There is little pressure to mislead or exaggerate, nor pressure on kin to ignore such signals. The egalitarian sex distribution and early maturation of human language make perfect sense in a kinselected context. In a kin-selected communication system, the earlier an offspring's communicative abilities mature, the better. In particular, a long-lived animal (e.g. most primates) which by trial and error acquires a large number of complex concepts over its lifetime, can increase its reproductive success by transferring its knowledge to its offspring, thus increasing their survival. The only intrinsic limit to the adaptive value of complexity in such a system is the complexity of the concepts themselves. Finally, kin selection solves the 'lone mutant' problem (who does a linguistic mutant communicate with?) neatly, since a mutant is quite likely to share novel alleles with its own offspring.

There are two main problems with this hypothesis. First, as any parent or sibling knows, conflict among kin is not uncommon (Trivers 1974), especially where resources are limited and kin do not disperse (Frank 1998). However, potential problems associated with sibling rivalry or parent-offspring conflict in language are much reduced by the fact that information is not a limited resource like food or nest sites. Because sharing information with one child does not mean less of it for the next, the effect of such sibling and parent/offspring competition is greatly reduced. A more serious problem with kin selection is that adult humans obviously do not speak only with kin. This seems best explained by ‘reciprocal altruism’ – the other major theoretical route to cooperative behavior (Price 1970, 1972; Trivers 1971; Dessalles 1998). The idea is succinctly captured by the saying ‘I’ll scratch your back if you scratch mine’. Despite the undeniable logic of reciprocal altruism, and its ubiquity in human interactions, it is surprisingly rare in nonhuman animals (Stevens and Hauser 2004). Indeed, almost all putative nonhuman examples are among kin. However, the logical benefits of reciprocal altruism becomes almost unavoidable once a low-cost, unlimited communication system with the potential for honest information transfer has evolved via kin selection. Although avoiding the ‘free rider’ problem raises certain difficulties (Dunbar 1996), cognitive mechanisms for Machiavellian intelligence were already in place in the LCA and primates in general (Byrne and Whiten 1988) that might have abetted this problem. Crucially, a kin-selected communication system could pave the way to a reciprocally-altruistic information transfer among non-kin without any further genetic change, but the converse is not true. Thus, kin selection appears to offer a clear, viable route to an honest, low-cost signaling system like language, one that avoids most of the problems facing a sexual-selection account (Fitch 2004). Given this excellent fit between kin selection and the most unusual features of language, it is surprising that kin communication has been almost entirely neglected as an important force in language evolution. Perhaps one reason is the too-frequent equation of ‘reproductive success’ with mating success. These are not equivalent. For primates, and females of the ape/human lineage in particular, having sex is the easy part, and helping highly dependent offspring survive their long childhoods until maturity is a far more difficult challenge (one reason, perhaps, that language has not evolved among songbirds).

Testable predictions

Recapping the previous sections, we have considered three types of selection (natural, sexual and kin) and their associated functional hypotheses. These hypotheses (particular in combination) generate many testable predictions, some obvious and others less so. An already-mentioned example is that sexual selection predicts male bias and late maturation, while kin selection predicts female bias and early maturation. Kin selection also predicts, under conditions resembling those of early hominids, that the transfer of valuable information

should be preferentially among kin, a prediction that has already received some empirical support (Nettle and Dunbar 1997). The ‘better language for better thought’ hypothesis invites various experimental tests as well: do humans exposed to a complex task perform better if induced to create (private) names for all of the tasks’ components? Do children remember an object better if given a name for it? Work in the Sapir – Whorf tradition can help clarify such issues. Such empirically-testable predictions illustrate the value of positing explicitly functional hypotheses in biolinguistics: they can lead us to collect or examine data not otherwise recognized as being relevant.

Phylogenetic paths to language

In the context of language evolution, phylogenetic hypotheses have (and sometimes deserve) a bad reputation. Because language neither fossilizes (and so lacks direct paleontological data) nor has much in common with other species (presenting difficulties for comparative reconstruction), phylogenetic narratives are, at best, difficult to test. At worst, discussions of language phylogeny can degenerate into the spinning of fanciful fairytales and ‘just so stories’, and the similarity of such narratives to the origin myths found throughout world cultures and religions does little to increase their scientific appeal. Nonetheless, I suggest that phylogenetic narratives, when constructed with proper attention to comparative data and evolutionary theory, and constrained by current knowledge of mechanism, function and ontogeny, can sometimes provide a useful theoretical framework for asking questions about language evolution. In particular, good phylogenetic hypotheses will generate testable empirical hypotheses that will enrich our understanding of language on all levels, and can represent one important component of a future theory of language evolution. Although the majority of phylogenetic hypotheses are too speculative and ill-defined to make testable predictions, and the field would do well to overcome its apparent obsession with such narratives as the central question of the biology and evolution of language, they do have a role to play in a complete understanding of language evolution. Here I will discuss some of the theoretical issues involved, and end by briefly considering a few current hypotheses.

Preadaptation, exaptation and spandrels

As recognized clearly by Darwin, evolution lacks foresight, and old structures are often put to new uses, a phenomenon traditionally termed preadaptation. Classic examples include the conversion of jaw bones of ancestral reptiles to the middle ear ossicles in mammals, or the conversion of the gill bars of ancestral fish to the tetrapod larynx. For this reason, it is critical to avoid confusing the current utility of a trait (the function it serves in extant individuals) with its

past function(s) during phylogenesis. Gould and Vrba (1982), suggesting that the term preadaptation connoted foresight, and coined a new term – ‘exaptation’ – for old traits put to new use (or the process by which this occurs). Unfortunately, the ubiquity of evolutionary ‘tinkering’ and the reuse of old functions (Jacob 1977) means that virtually any trait once served a different function, if a long enough view is taken. Thus, their suggested broad interpretation would typically force us to replace the term ‘adaptation’ with ‘exaptation’ across the board. To avoid this, most theorists use the term ‘exaptation’ in a narrower sense, to pick out the (typically shortlived) period in a trait’s evolution when it is being put to new use, but has not yet been selected to support this new function (e.g. Briscoe 2003). Following (Gould and Lewontin 1979), an important subset of such traits are often termed ‘spandrels’. A spandrel is an unselected by-product of some other selected trait, which is put to a novel use. Spandrels clearly exist (despite the utility of noses for supporting eyeglasses, they are clearly not adaptations for this function), but their relative frequency remains controversial (Dennett 1995). In general, if the new exaptive function is important for survival, and variance exists, spandrels and other exaptations will quickly be modified to better serve their new function, and thus cease to be exaptations. The process of exaptation will thus be quick, and a trait’s typical tenure as a spandrel correspondingly brief. Thus, evolution will cycle from adaptations to exaptations (when the new function is implemented), and subsequent selection in the new context will generate, once again, an adaptation (which in hindsight may serve as a preadaptations for a new function).

Is language a spandrel? From the perspective advocated here, fractionating language into multiple interacting components, it is clear that the mechanisms compromising the FLB as a whole cannot be a spandrel. Language serves vital functions among contemporary humans, and bears all the marks of an adaptation (including early and robust development, specific alleles associated with linguistic components, etc. (Lieberman 1984; Pinker and Bloom 1990)). However, when we ask the same question of particular components of the language faculty, it becomes an empirical question to be decided on a case-by-case basis. For something as recently evolved as language, and given the abstractness of many characteristics of language that interest linguists (such as recursion or subadjacency), it would be surprising indeed if none of them were spandrels, in the sense of remaining unchanged from an initial exapted state. Thus, turning the question around, if we ask whether *any* aspects of language are spandrels, the answer is almost certainly ‘yes’ – as true for most aspects of biology like digestion or circulation. Various aspects of phonology must derive from traits of the mammalian vocal and perceptual system which clearly did not evolve ‘for’ language (MacNeilage 1998b). Despite the utility of teeth for making dental consonants, there is no sign that they were selected for this specific function. Similarly, many aspects of the primate conceptual system predated language, and have not obviously changed since the LCA (Seyfarth and Cheney, in press). To take a more controversial example (Pinker and Jackendoff 2005; Fitch et al.

in press), let us accept for the sake of argument the hypothesis that the human ability to perform linguistic recursion (embedding structure within structure) derives phylogenetically and mechanistically from an earlier ability of the LCA to do complex social mind reading (recursively embedding propositions about the mental states of others: ‘John knows that Susan wants Jack to accompany her’) (Worden 1998; Hauser et al. 2002a; Seyfarth et al. 2005). While such an ability, by hypothesis, was clearly put to new use in a linguistic context (‘this must be the lion that ate that gazelle that I was stalking yesterday’) it is not immediately obvious that such a new use would entail any new selective forces or changes of the preexisting ability. To demonstrate empirically that linguistic recursion is not a spandrel, we would need to show that it both functionally entails, and mechanistically exhibits, characteristics not found in social mind-reading recursion. These examples illustrate a foundational principle of modern evolutionary theory: that adaptation is ‘an onerous concept’ which must be demonstrated rather than assumed (Williams 1966). Theorists who ignore this point risk reducing their ideas to Panglossian caricatures of evolutionary thinking (Gould and Lewontin 1979; Gould 1991).

Dual-stage, analytic and synthetic theories

To end, I will discuss a few current phylogenetic hypotheses in more detail, all of which take the LCA as their starting point, and end up with full modern human language. The complexity of the FLB makes any ‘single cause’ or ‘Big Bang’ theory of language evolution dubitable. To take an old example, the ‘bowwow’ theory of language origins suggests that vocal imitation of animal sounds provided a starting point for language evolution. While such a process might provide some impetus for vocal imitation, and perhaps even some primitive referentiality, it can’t explain the evolution of unlimited propositional semantics, or of complex syntax. In general, modern theorists agree on the necessity of some variant of a multi-stage evolutionary scenario, positing an initial stage human evolutionary history in which a prelinguistic communicative system, a ‘protolanguage’, evolved. Protolanguage shared certain characteristics with modern language, but lacked some other features. The evolution of protolanguage could theoretically have been driven by selective forces differing from modern language (e.g. sexual vs. kin selection). Beyond the general agreement on the necessity of multiple stages, however, there are a wide variety of models in the literature, with quite different notions of what such a protolanguage might have been like.

A key distinction among currently-available hypotheses of protolanguage is the analytic/synthetic distinction, which concerns the timing and nature of the evolution of the complex form/meaning pairings that underlie the lexicon, syntax and semantics (Hurford 2000). ‘Synthetic’ models, assumed by many authors (Bickerton 1990; Jackendoff 1999), posit that protolinguistic utterances consisted of either single words, or simple concatenations of words, without

additional phrasal structure. By such models, the lexicon and reference came first, and the leap from protolanguage to modern language came with the addition of syntactic structure at the sentence level. This fits with the intuitive notion of cavemen grunting monosyllables around the fire, and the observation that young children typically begin their linguistic careers by uttering single words, with multiword sentences following. In contrast, ‘analytic’ models (also termed ‘holistic’ or ‘holophrastic’) posit the contrary: that the initial pairing between meaning and form mapped entire propositions to complex but undecomposable forms. In such models, complex form (à la music, or birdsong, possessing phrase structure but devoid of compositional meaning) preceded ‘words’ in the modern sense (Arbib 2003). Despite being non-intuitive, there is increasing evidence that such models should be taken seriously (Wray 2002). First, studies of child language acquisition suggest that children’s one-word utterances in fact map to whole propositions (e.g. the infant’s ‘up’ means ‘please pick me up’ and is certainly not identical to the adult’s meaning of the preposition ‘up’). Second, even adult language is full of holophrasis (Jackendoff 1999; Wray 2002), and the adult lexicon contains many phrases with undecomposable form/meaning pairings (e.g. ‘abracadabra’ for the revealing of a magic trick, or ‘kick the bucket’ as ‘to die’). Finally, the comparative data reviewed above suggest that it is easier to evolve complex learned structure in a vocal communications system (as evidenced by the multiple parallel evolution of such structure in birds and whales) than to evolve a system of combinatoric meaning. For these reasons, there is an increasing tendency to take analytic models seriously, and synthetic hypotheses can no longer be simply assumed without argument (see, e.g. Arbib 2003; Bickerton 2003).

Any theory of language evolution that starts with learned vocal signals, and a large lexicon of form/meaning pairs, has already assumed much of what needs to be explained, since the comparative data clearly indicates that the LCA had neither of these (Seyfarth and Cheney, in press). Surprisingly few theorists have attempted to outline an explicit phylogenetic sequence, from the LCA to modern humans. I now review three dual-stage phylogenetic hypotheses for language evolution which do so, each positing a distinct form of protolanguage: either asyntactic words, gestural communication, or a music-like protolanguage. This is far from a comprehensive review. Many other models focus on just one stage and do not attempt to be complete, while others include as many as seven stages (e.g. Jackendoff 1999; Arbib 2003). Other valuable models focus on a single intermediate stage in detail, and even with this limit, exploring the implications of available data can require a book length treatise (for examples see Donald 1991; Deacon 1997). The models below are chosen to give the flavor of current approaches that start with a reconstructed LCA and end with modern language.

Asyntactic protolanguage

Derek Bickerton, a linguist specializing in creoles, has been writing about language evolution since 1981, consistently and correctly urging a more serious

attention to the complexity of syntax. Bickerton has advanced a widely-discussed synthetic dual-stage model, and is apparently the first to use the term ‘protolanguage’ in an evolutionary context. Bickerton’s model is intuitive, suggesting that protolanguage was composed of simple utterances (of one to a few words), and can be thought of as a lexicon with no sophisticated syntactic structure. Bickerton says little about the evolution of this first stage, perhaps assuming that something like his ‘protolanguage’ existed in the LCA. Current understanding of private calls, especially “functionally referential” calls, suggests that attaining protolanguage is an important hurdle, first because monkey alarm calls are not learned, and thus are not extensible to an indefinite vocabulary, and second because they lack intentional referentiality (Seyfarth et al. 2005). More recently, (Bickerton 2000) has articulated a model of syntactic evolution which take as its starting point semantic structures (particularly those pertaining to social cognition: ‘who did what to whom’) as the preadaptive basis for syntactic argument structure, a very plausible argument. Bickerton presents little discussion of the selective forces behind either stage, apparently assuming that syntax arose in a sexually selected context: ‘females would surely have preferred mates whose communicative capacities so strikingly outclassed those of other available partners’ (Bickerton 1998, p. 353). As reviewed above, modern evolutionary theory suggests that this is a dubious assumption. Despite these difficulties, a more articulated version of Bickerton’s hypothesis (which sheds any referential call precursor assumption, devotes more attention to the evolution of protolanguage, and incorporates kin selection) seems likely to remain a leading synthetic model for language phylogeny (see Carstairs-McCarthy 1999; Jackendoff 1999; Bickerton 2003).

Gestural protolanguage

Over the centuries many authors have speculated that protolanguage was either wholly or mostly composed of facial and manual gestures, speech being a later addition (for some history see Hewes 1973). This hypothesis was rendered more plausible by the discovery that apes are considerably better at communicating via manual gestures than speech (Gardner and Gardner 1969). Ongoing studies of natural gestural communication in apes supports this idea (Tomasello 2003). Michael Corballis, a prominent current champion of this idea (Corballis 2003) even suggested provocatively that speech was a recent innovation, purely cultural, on a par with writing systems (although the FOXP2 data has led him to repudiate this view, Corballis pers. comm.). The gestural hypothesis is consistent both with the general co-existence of gestures with speech in all world languages, and with the fact that signed languages are full, complete languages (itself a relatively recent insight: (Klima and Bellugi 1979; Emmorey 2002)). While the gestural hypothesis neatly solves the continuity problem between the LCA and hominids with protolanguage, it raises a new continuity problem between gestural protolanguage and modern spoken language (MacNeilage 1998a). What selective forces and adaptive path could transform a fully-functional signed system into a spoken system (particularly

given the lack of vocal imitation in the LCA)? While speech is indubitably more useful in communicating around corners, in darkness, or while holding tools, it is not obvious that these pressures are powerful enough to drive a novel, spoken system. Critiques of the gestural hypothesis are given by Tomasello (2002) and MacNeilage (1998a), while Arbib (2003, 2005), Corballis (2003) defend and further elaborate it.

Neurophysiological findings with nonhuman primates have recently been cited as additional support for the gestural hypothesis: the discovery of a class of neurons in the frontal cortex, called 'mirror neurons', that show increased activation both when the monkey performs some manual action (say grasping a nut) and when it sees that same action performed (di Pellegrino et al. 1992; Rizzolatti and Arbib 1998). There are three reasons many researchers find this discovery exciting. First, as previously mentioned, imitation is a key ability underpinning any human language, and mirror neurons have just the computational properties that would be required for a visuo-manual imitation system. Unfortunately, macaques have very limited manual imitation abilities (Whiten and Ham 1992; Tomasello and Call 1997; Subiaul et al. 2004), suggesting that whatever function mirror neurons serve, it is not imitation. Second, because mirror neurons function in the manual domain, they have been claimed as support for gestural origin theories of language evolution (Corballis 2003). But mirror neurons would provide support for a 'hands first' hypothesis of language phylogenesis only if their auditory equivalents (matching produced sounds with perceived sounds) did *not* exist. But an audiovocal analog of the mirror system apparently exists (Fadiga et al. 2002; Kohler et al. 2002), making this claim unjustified. Finally, the specific location of mirror neurons in the primate brain, in a site analogous to Broca's area in humans, is the most compelling reason for the interest in mirror neurons. Although Broca's area is clearly not the only part of the brain involved in language production (for an extended critique see Lieberman 2000), there is little doubt that it does play an important role in many aspects of both speech production and comprehension (especially syntax processing (e.g. Friederici et al. 2000)). Thus, more recent explorations of mirror neurons in relation to language evolution focus on their role as preadaptive precursor mechanisms for capabilities that are clearly required for language (Arbib 2003, 2005).

Prosodic protolanguage

Darwin posited (Darwin 1871) that the earliest stage of language evolution was musical, in the sense of incorporating complex, learned vocalizations, but with no propositional meaning (or perhaps a holophrastic form/meaning pairing, as for courtship songs, war songs, dirges and the like). Because this 'musical' protolanguage was, by hypothesis, the common ancestor of both modern language and modern music, we should not assume that it was identical to contemporary music. Instead, I suggest the term 'prosodic protolanguage'. By analogy with the comparative method, the properties of this version of protolanguage would include the two main properties that modern human lan-

guage and music share: a focus on the vocal/auditory channel, and complex structure that is learned and thus culturally transmitted. Darwin assumed, based on comparative evidence from birds, that sexual selection drove the evolution of this prosodic protolanguage: 'I conclude that musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex'. This proposed function is clearly compatible with the comparative data (not just for birds, but also marine mammals): vocal learning of complex structured signals without propositional meaning has evolved repeatedly among vertebrates, typically under sexual selection (Fitch, in press). If we add to Darwin's prosodic protolanguage a second stage, in which kin communication drove the addition of a fully propositional and intentional semantics (see above, and Fitch 2004) a plausible analytic dual stage hypothesis results. By this hypothesis, music is essentially a behavioral 'fossil' of an earlier human communication system, remaining a human universal for historical reasons. The relaxation of selection due to the advent of spoken language renders understandable the uneven distribution of musical skill among individuals, contrasting sharply with the ubiquitous, robust and genetically-canalized development of language. The main difficulty for this hypothesis is shared by any analytic hypothesis: that it leaves unexplained the transition from a holistic meaning system to a decomposable one. See (Donald 1991; Brown 2000; Fitch, in press) for further discussion.

Testable predictions

The phylogenetic hypotheses reviewed above are of course impossible to test directly, but there are multiple sources of converging data that can render them more or less plausible, especially when considered simultaneously, as alternatives. For instance, the gestural hypothesis retrodicts the ubiquity of human gesture and the existence of signed languages, while the prosodic hypothesis explicates the existence and ubiquity of music. However, both generate novel predictions as well. If musical ability provided the mechanistic precursor for spoken language, then musical ability today should co-vary with phonological ability (e.g. ability to perform tongue-twisters, imitate vocally, and acquire new dialects or languages without accent). Further, the neural mechanisms involved in these tasks should be similar, and the genes associated with these abilities the same. However, non-speech language abilities (semantics and reference related component of syntax, such as anaphora) should be disjunct: these evolved on top of, and in addition to, prosodic protolanguage. Here the wide variance among humans in musical abilities combines with the many formal similarities in music and language to provide a valuable empirical wedge into the problem. In contrast, the gestural hypothesis predicts no correlation between gestural and phonological abilities, or the neural and genetic bases for these, since speech abilities supplanted manual/visual imitation rather than exapting them, while predicting strong overlap between gestural and spoken mechanisms for syntax and semantics (Klima and Bellugi 1979; Emmorey 2002). By exploring the empirical consequences of different phylogenetic hypotheses, we can not

only test them, but discover independently interesting things about the genetic mechanisms underlying language (and music, gesture, etc). Such empirical tests are the best (some might say the only) justification for phylogenetic hypothesizing, and provide some hope for improving the poor reputation of such theorizing.

Conclusion and prospects

In conclusion, by any measure, the study of the evolution of language represents an exciting and rapidly growing field, and problems that have long fascinated philosophers and scholars are finally beginning to yield to empirical study. The uniquely interdisciplinary nature of biolinguistics certainly poses problems: discussion is still often marred by misunderstanding and unproductive bickering. Nonetheless, a growing community of scientists of diverse backgrounds, including linguists, evolutionary biologists, neuroscientists, anthropologists, computer scientists and molecular biologists, are overcoming these difficulties through collaboration and mutual respect. Although questions still vastly outnumber answers, there is good reason for optimism that progress can be made on problems that have tantalized thinkers for millennia. Already substantial progress has been made both at achieving consensus on the core questions that face any theory of language evolution, and on the data relevant to answering these questions (Christiansen and Kirby 2003). After years of neglecting evolution, linguists are rolling up their sleeves and forming productive collaborations with biologists and cognitive scientists, and the valuable insights of decades of theoretical and comparative research are being re-integrated into the cognitive sciences and comparative biology (Rizzolatti and Arbib 1998; Calvin and Bickerton 2000; Jackendoff 2002; Hauser et al. 2002a). Areas of particular excitement include the search for genes linked to language (of which FOXP2 is only the first), the further exploration of precursors to language in nonhuman primates and other animals (at neural, cognitive and behavioral levels), and the further development of an integrated theoretical framework (both conceptual and mathematical) capable of encompassing the many complex issues that an eventual theory of language evolution must resolve. Comparative data will continue to play a fundamental role in this endeavor, and interdisciplinary collaboration, theoretical clarification, and empirical testing will be important in furthering this progress.

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