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Author(s): Alex Mesoudi, Alan G. McElligott, and David Adger
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Introduction: Integrating Genetic and Cultural Evolutionary Approaches to Language

ALEX MESOUDI,[1] ALAN G. MCELLIGOTT,[1] AND DAVID ADGER[2]

Abstract The papers in this special issue of *Human Biology* address recent research in the field of language evolution, both the genetic evolution of the language faculty and the cultural evolution of specific languages. While both of these areas have received increasing interest in recent years, there is also a need to integrate these somewhat separate efforts and explore the relevant gene-culture coevolutionary interactions. Here we summarize the individual contributions, set them in the context of the wider literature, and identify outstanding future research questions. The first set of papers concerns the comparative study of nonhuman communication in primates and birds from both a behavioral and neurobiological perspective, revealing evidence for several common language-related traits in various nonhuman species and providing clues as to the evolutionary origin and function of the human language faculty. The second set of papers discusses the consequences of viewing language as a culturally evolving system in its own right, including claims that this removes the need for strong genetic biases for language acquisition, and that phylogenetic evolutionary methods can be used to reconstruct language histories. We conclude by highlighting outstanding areas for future research, including identifying the precise selection pressures that gave rise to the language faculty in ancestral hominin species, and determining the strength, domain specificity, and origin of the cultural transmission biases that shape languages as they pass along successive generations of language learners.

The papers in this special issue of *Human Biology* originate from a Centre for Ecology and Evolution symposium held at Queen Mary, University of London in 2009. As our title suggests, the aim of the symposium was to attempt to link two areas of language research that have received increasing interest in recent years, yet in our view have not been sufficiently integrated with each other. The first concerns the study of the genetic evolution of the language faculty (i.e., when, how, and why the capacity for language evolved in our species' evolutionary

[1] Biological and Experimental Psychology Group, School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom.

[2] Department of Linguistics, Queen Mary University of London, Mile End Road, London E1 4NS, United Kingdom.

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past). For a long time, efforts to answer such questions have been hindered by the inconvenience that spoken language does not fossilize, and because language has traditionally been seen as an entirely human-unique trait. Yet in recent years, a wealth of new comparative data from a range of nonhuman species has challenged the latter assumption (Hauser et al. 2002), while new methods of genetic analysis (e.g., Enard et al. 2002) and neuroimaging techniques (e.g., Petkov et al. 2008) have begun to explore the genetic and neural basis of language, aiming to shed light on its evolutionary function and origin. The second field receiving increasing attention concerns the cultural evolution of specific languages, once the language faculty is in place. As noted by Darwin (1871), language change can be viewed as an evolutionary process of descent with modification, broadly similar to, and acting in parallel to, genetic evolution (see also Brighton et al. 2005). While this remained for many years merely an interesting analogy, recently several researchers have begun to use quantitative evolutionary methods from biology to understand language change. Phylogenetic methods have been used to reconstruct language histories (Pagel 2009), providing a rigorous, quantitative means of reconstructing historical linguistic developments based on an extension of the traditional methods of historical linguistics, while evolutionarily inspired computational models and lab experiments have been used to explore whether languages might themselves be subject to evolutionary pressure constrained by brain structure and function (Christiansen and Chater 2008).

Collectively, these two fields of research can potentially be seen as placing the study of language within an integrated evolutionary framework, using the same Darwinian principles and methods to explain both the origin and gradual evolution of the language faculty over millions of years, and short-term language change over decades and centuries. Yet such a claim would be premature, and several fundamental questions remain to be answered. Many of these questions lie at the intersection of genetic and cultural evolutionary processes. The following sections summarize the two fields, placing the contributions in this special issue within the context of the wider literature, before drawing links between the two fields with future outstanding issues in mind.

Genetic Evolution of the Language Faculty: A Comparative Approach

Spoken language does not fossilize. Nor do the neural mechanisms underpinning the language faculty, or even the structure of the vocal tract. This severely limits any attempt to use the fossil record to infer when, how, and why the language faculty evolved in the hominin lineage (Fitch 2000). An alternative approach is to study the vocal, perceptual, communicative, and cognitive processes of other extant species (Hauser et al. 2002). While no other extant species has fully human-like language, a surprisingly large number of species have been shown to exhibit components of human language, and these data are beginning to provide a picture of the evolutionary history and function of language-related traits.

The key benefit of comparative studies is the identification of homologies and analogies: where a language-related trait is exhibited exclusively by a group of closely related species (e.g., all primates), then we can infer that this trait evolved in the common ancestor of these species and has been inherited by each (i.e., it is homologous). If, on the other hand, a trait is exhibited by a set of distantly related species (e.g., humans, birds, and whales), we can infer that the trait evolved independently on a number of separate occasions (i.e., it is analogous). Identifying the common social or ecological environments of these distantly related species might then tell us about the evolutionary selection pressures that caused the trait to emerge and persist.

Fedurek and Slocombe (this issue) take the first approach, reviewing research on the vocalizations of nonhuman primates. They identify several traits that humans share with other primates and so are indicative of common descent. For example, functional reference, where signals refer to external objects or events, is exhibited in the alarm calls of several primate species in response to specific predators, as well as calls that convey information about food quality and conspecifics (e.g., their mating status, relatedness, or dominance) (e.g., Slocombe and Zuberbühler 2005). Some monkey species also exhibit potential precursors to the tight relationship obtaining between meaning and structure that is found in human languages, in cases where the addition of a generic call modifies the meaning of a specific predator alarm call, or where the sequence of calls rather than their type affects meaning (Arnold and Zuberbühler 2008). Yet Fedurek and Slocombe also identify key differences between human and nonhuman vocalizations: the latter are more inflexible, have a far more limited range, and are less subject to flexible modification by learning than the human vocal repertoire.

Wilson and Petkov (this issue) complement behavioral research with new findings from neuroimaging studies of primate vocalizations. Supporting the behavioral findings that human speech did not evolve entirely de novo in the hominin lineage and has several precursors in nonhuman primates, Wilson and Petkov present evidence that humans, chimpanzees, and macaques all process vocal information in the same parts of the superior temporal lobe (e.g., Petkov et al. 2008) and that there are no highly localized, language-specific brain regions in the human brain that are entirely absent from nonhuman primate brains. Yet there are also interesting cross-species differences, such as that humans and chimpanzees process vocal information in lower parts of the temporal lobe than macaques, suggesting some evolutionary changes since the split of the great apes from other primates.

Beckers (this issue) reviews research into the vocal and perceptual abilities of songbirds. Whereas language-related traits shared by humans and other primates are likely to be shared because of descent from a common ancestor, any similarities between human and bird vocalizations are likely attributable to independent evolution in separate lineages. Beckers shows how humans and birds show surprising similarities in their vocal abilities, with the latter exhibiting phonetic discrimination and categorical perception rivaling that of humans. And unlike nonhuman primates, birds show flexible vocal production attributable to fine-controlled vocal tracts and vocalizations that are learned rather than genetically fixed. As Beckers notes, this tells us, first, that flexible vocal production and vocal learning do not inevitably lead to the evolution of human-like language, given that none of the 4,000 extant songbirds have evolved human-like language in the 50 million years since vocal learning first evolved. And second, given that birdsong is a sexually selected trait, the similarly flexible vocalizations of humans may have evolved in the hominin lineage in the last 6 million years not for predator-avoidance or food-related functions (as seen in nonhuman primates) but for attracting mates. Perhaps the human language faculty represents an improbable combination of fine-grained sexually selected vocal abilities and the precursors of functional reference and syntax identified by Fedurek and Slocombe in nonhuman primates (but which are absent in songbirds).

Despite the presence of these analogous and homologous prelinguistic traits in a range of other species, the fact remains that the human language faculty differs in several ways from nonhuman communicative capacities. Given that nonhuman primates raised in the same environments as human children fail to acquire human-like speech and language (Terrace et al. 1979), a substantial part of this difference must be genetic in origin. Indeed, recent advances in gene sequencing technology have begun to yield insights into the underlying genetic basis of the human language faculty. A significant discovery was the identification of the FOXP2 gene, mutations of which cause severe impairment to speech production and grammar (Enard et al. 2002; Fisher and Scharff 2009). Comparative genetic analyses have revealed similar forms of the FOXP2 gene in various vertebrate species including nonhuman primates and songbirds, supporting the behavioral and neurobiological findings reviewed above that human language has precursors in other species (Fisher and Scharff 2009). Interestingly, analyses suggest that the current human version of FOXP2 emerged around 200,000 years ago, coinciding with the appearance of anatomically modern humans (Enard et al. 2002). Yet FOXP2 is far from the single "gene for language": FOXP2 has also been implicated in motor control and neural plasticity functions that are not language-specific, while genes other than FOXP2 have been implicated in language function (Fisher and Scharff 2009).

Brown (this issue) takes advantage of these new genetic data to test an intriguing hypothesis for the evolution of the language faculty. Brown proposes that language evolved as a consequence of genomic imprinting, where genes are preferentially expressed depending on whether they are inherited paternally or maternally. According to this parental antagonism theory (Haig 1997), genes that are preferentially expressed when inherited paternally should increase costs to the offspring's mother to their own benefit, while genes that are preferentially expressed when inherited maternally should reduce costs to the mother. Brown consequently argues that language evolved for two functions. First, as a means for offspring to elicit resources from their parents, predicting that these exploitative functions of language (e.g., infant crying as requests for food) should be determined by paternally expressed genes. And second, as a means of fostering cooperation between mother and offspring, predicting that these cooperative functions of language (e.g., infant cooing indicating satiation) should be determined by maternally expressed genes. Consistent with this hypothesis, Brown shows that a high proportion of imprinted genes, including the aforementioned FOXP2, have been implicated in language-related functions despite their overall rarity in the human genome.

Cultural Evolution of Languages: A Curious Parallel

The previous section concerned the genetic evolution of the language faculty in the hominin lineage over the last several million years. Moving forward in time, we can also explore, once the language faculty is in place, how specific languages (e.g., English or Urdu) change over much shorter timescales of decades and centuries, and how languages have diversified into the almost 7,000 extant languages spoken worldwide. It has long been noted that the process of language change bears a striking resemblance to the biological evolution of species (van Wyhe 2005): as Darwin himself remarked, “The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel” (Darwin 1871:90). Recently, several groups of researchers have gone further than simply noting a “curious parallel” and used evolutionary concepts, methods, and tools developed by biologists to analyze language change, as part of a broader science of cultural evolution (Mesoudi et al. 2006).

The authors of two of the contributions, Smith (this issue) and Christiansen, Reali and Chater (this issue), argue that one implication of viewing language as an evolutionary process is that language itself may adapt to general-purpose, non-language-specific features of cognition. Whereas traditional nativist theories explain apparent language universals as resulting from an innate, language-specific universal grammar (Chomsky 1965), these contributors argue that similarities across languages result from shared non-language-specific aspects of cognition generating similar selection pressures on languages as they are learned by each new generation. Smith (this issue) reviews both computational models and laboratory experiments (e.g., Smith and Wonnacott 2010), which demonstrate how what may appear to be weak learning biases in single individuals can have strong population-level effects when repeated over successive generations of learners. This is akin to how even very weak selection pressures operating in biological evolution can have strong multiple-generation effects, such as when alleles with only a small (1–2%) selective advantage over other alleles are driven to fixation surprisingly quickly (Fisher 1930). Consequently, Smith argues that any observed strong cross-language universals may not necessarily result from strong, innately specified, language-specific biases and may result instead from weak, non-language-specific biases. Christiansen, Reali, and Chater (this issue) make a corresponding argument based on similar computational models of language evolution (Chater et al. 2009). However, in this paper they show that while this conclusion holds for arbitrary features of language, for functional features of language a “Baldwin effect” may occur where linguistic features that are originally learned subsequently become genetically fixed to reduce learning costs. As evolutionary models of language evolution increase in sophistication, no doubt more refined predictions will be made concerning the precise mapping between individual cognitive biases and macroevolutionary language change.

Dediu (this issue) also discusses the relation between individual learning biases and language diversity, describing a recent case study showing a potential causal link between two genes related to brain development, ASPM and Microcephalin, and the distribution of tonal languages, with tonal languages spoken by populations with high frequencies of these genes and nontonal languages by populations with low frequencies (Dediu and Ladd 2007). Dediu suggests that this particular aspect of linguistic diversity has been shaped by weak biases determined by these particular genes: “weak” because tonal and nontonal languages can be learned by people both with and without the genes; it only affects the ease of learning and only has strong effects over several generations of language acquisition.

Finally, Jordan (this issue) uses phylogenetic comparative methods to reconstruct the evolutionary history of kinship terminology in the Austronesian language family. Phylogenetic methods were originally developed in biology to reconstruct the evolutionary history of species. Given that cultural change constitutes a similar system of descent with modification, several researchers have recently applied phylogenetic methods to cultural data sets (Mace et al. 2005), including languages (Pagel 2009). As Jordan notes, phylogenetic methods are particularly useful when comparing data across societies because they explicitly control for descent: if two societies share the same traits (in this case, kinship terminologies) because they both inherited it from the same ancestral society, then they cannot be treated as independent data points and any cross-cultural comparison will be confounded. Phylogenetic comparative methods explicitly control for such spurious historical confounds (known in anthropology as “Galton’s problem”). Jordan shows that the ancestral state of Austronesian kinship terminology was one which delineated relative age (e.g., different terms for older vs. younger siblings) but not relative sex (e.g., different terms for same-sex vs. opposite-sex siblings). Further analyses showed different probabilities of subsequent shifts between different terminologies. Jordan’s study represents a valuable addition to the phylogenetic reconstruction of language histories (Gray and Atkinson 2003; Gray and Jordan 2000) and shows how evolutionary tools can be used to address longstanding issues in cultural anthropology and linguistics, in this case regarding the origin and current distribution of kinship terminology.

Conclusions: Toward Integration

It is evident from the broad-ranging contributions to this special issue that an adequate understanding of a phenomenon as complex as language requires a range of methods spanning several disciplines, including genetic sequencing, neuroimaging, computational modeling, laboratory experiments, comparative studies of nonhuman behavior, and cross-cultural comparisons. As the contributions demonstrate, much progress has been made in recent years. Nevertheless, several fundamental questions remain (see also Fitch, this issue, who provides a more detailed overview of the following issues).

First, while comparative studies of nonhuman primate communicative abilities have identified several potential homologous precursors to language, such as functional reference, and analogous traits, such as the flexible vocal production and vocal imitation of songbirds, the precise selection pressures that gave rise to the human language faculty in the hominin lineage in the last six million years remain unclear. The analogies with birdsong noted by Beckers (this issue) suggests a potential role for sexual selection, while the relatively advanced social abilities of primates as a group (Byrne and Whiten 1988) may provide especially pronounced selection pressures for high capacity communication systems such as language (Dunbar 1996). Fedurek and Slocombe's (this issue) observation that nonhuman primate functional reference applies not only to survival-related stimuli (e.g., predator threats and food quality) but also social stimuli (e.g., whether a caller is aggressor or victim in an antagonistic interaction) might support this notion that language evolved to communicate information about social relationships rather than non-social knowledge (see also Mesoudi et al. 2006). Yet as Brown (this issue) points out, the cooperative basis of language must be explained, not assumed. The evolution of human cooperation is currently a highly contentious topic (Gintis et al. 2003; Mesoudi and Jensen in press), and evolutionary theories of the origin of the language faculty will need to take such issues into account. Brown's own parental antagonism theory of language evolution is innovative in this respect, and also in its use of recent genetic data, and his study points the way to a fuller integration of genetic data and evolutionary theory.

Jordan's (this issue) study of kinship terminology illustrates the value of borrowing methods from biology to analyze language change, in this case phylogenetic comparative methods. This was justified by the assumption that language change constitutes a similar Darwinian evolutionary process of descent with modification to the genetic evolution of species (Mesoudi et al. 2004). Yet interesting questions might be asked about the extent to which the microevolutionary processes driving cultural evolution are equivalent to those driving biological evolution: whereas genetic inheritance involves the all-or-nothing transmission of discrete genetic particles, speech sounds appear more likely to blend together in a continuous manner, and cultural microevolution exhibits processes such as conformity and prestige bias that do not have clear parallels in biological evolution (Richerson and Boyd 2005). A related question is the extent to which linguistic evolution is similar to other forms of cultural evolution, such as the evolution of material artifacts or social institutions, in such properties as fidelity of transmission or mutation (innovation) rate, and how evolutionary methods can be modified in order to take such differences into account.

The papers by Smith (this issue), Christiansen et al. (this issue), and Dediu (this issue) all concern what is becoming a heated debate over the extent to which universal properties of language can be explained by a domain-specific language acquisition device that immediately structures the input into a particular kind of system (Chomsky 1965) or by domain-general biases that are reified in the linguistic system by the repeated transmission of language to successive generations of language learners, as advocated by these contributors. As acknowledged by the contributors, much work needs to be done to determine exactly what these biases might be: are they genetic, as in the case of Dediu's (this issue) proposed genetic bias that favors nontonal languages over tonal languages, or are the biases themselves learned? If they *are* genetic, then can the evolutionary theories of language origins discussed above (e.g., the social brain theory or parental antagonism theory) be used to predict the form that such biases take? How specific are these biases to language? If they are not language-specific, then what domain-general functions do they serve? Could such a model apply to all aspects of language, or, as Christiansen et al. suggest, does the bias hypothesis apply only to arbitrary and not functional aspects of language? Exactly how strong or weak are these biases? Methods from evolutionary biology used to quantify the strength of natural selection (see Endler 1986) might be adapted to answer the latter question concerning the equivalent strength of cultural selection. The role of biases might also be addressed comparatively. A recent experimental study of zebra finches (Feher et al. 2009) showed that birds reared in isolation sing abnormal songs, but when this abnormal song is repeatedly learned by successive generations of birds then normal, species-specific song characteristics gradually emerge; this is a potential example of how a weak genetic bias can have strong multiple-generation consequences and is also consistent with the bias being domain-specific.

More broadly, the work in linguistic theory conducted over the past 50 years provides a rich resource of phenomena that can be used to test the plausibility of the idea that weak biases may be strengthened over time and that these biases are domain-general. It is important here to distinguish between typological claims about widespread surface properties of language (e.g., claims about universal word order correlations or feature inventories: Evans and Levinson 2009) and theoretical claims about the nature of the cognitive system that might lead to such properties (for example that human language has syntactic categories, compositional semantics, or structure-dependent rather than string dependent processes). The question of how the explanatory potential of the different models (domain specific vs. domain general, biases vs. strong-constraints) might map to these different kinds of linguistic properties is wide open.

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Guest Editors

ALEX MESOUDI is a lecturer in psychology in the School of Biological and Chemical Sciences at Queen Mary University of London. His research interests lie broadly in the area of human cultural evolution, specifically in the experimental and theoretical simulation of cultural transmission. Previous research projects have involved the experimental simulation of cultural transmission in the archaeological record, transmission chain experiments revealing hierarchical and social biases in human cultural transmission, and theoretical analyses of cultural phenomena such as partible paternity and copycat suicide. He has published in many journals, including *Behavioral and Brain Sciences*, *Evolution*, *Evolution and Human Behavior, Proceedings of the Royal Society B*, and *Psychological Review*, and he has a forthcoming book entitled *Cultural Evolution*, to be published by University of Chicago Press (2011).

ALAN McELLIGOTT is a lecturer in organismal biology at Queen Mary University of London. His research interests include mammal vocal communication, cognition, sexual selection, and animal welfare. He has published widely in these areas. His interest in language evolution arises from his comparative research on vocal communication in various mammals and how this is related to our understanding of vocal communication in humans. He is an editorial board member of the *Journal of Zoology*. He has published in many journals, including *Animal Behaviour*, *American Naturalist*, *BMC Biology*, *Proceedings of the Royal Society B*, *Behavioral Ecology and Sociobiology*, *Ethology*, and *Behavioral Ecology*.

DAVID ADGER is a professor of linguistics at Queen Mary University of London. His primary interest is in the nature of the human syntactic capacity and its connection to both sound and meaning, but he also has worked on theoretical models of how these capacities are put to use in language variation and change. He is editor of the journal *Syntax* and of *Oxford Studies in Theoretical Linguistics*, and he is author of *Core Syntax* (Oxford University Press 2003); coauthor of *Mirrors and Microparameters* (Cambridge University Press 2009); coeditor of four other books/special issues; and has publications in *Language*, *Linguistic Inquiry*, and many other journals.