

Why Possibly Language Evolved

Peter J. Richerson & Robert Boyd

Human language has no close parallels in other systems of animal communication. Yet it is an important part of the cultural adaptation that serves to make humans an exceedingly successful species. In the past 20 years, a diverse set of evolutionary scholars have tried to answer the question of how language evolved in our species and why it is unique to us. They have converged on the idea that the cultural and innate aspects of language were tightly linked in a process of gene-culture coevolution. They differ widely about the details of the process, particularly over the division of labor between genes and culture in the coevolutionary process. Why is language restricted to humans given that communication seems to be so useful? A plausible answer is that language is part of human cooperation. Why did the coevolutionary process come to rest leaving impressive cultural diversity in human languages? A plausible answer is that language diversity functions to limit communication between people who cannot freely trust one another or where even truthful communications from others would result in maladaptive behavior on the part of listeners.

Keywords: cultural evolution; evolution of cooperation and language; evolution of linguistic diversity

1. Introduction

Humans are highly unusual animals in depending upon social transmission from others for acquiring most of their adaptations (Boyd & Richerson 2005, Richerson & Boyd 2005), including the specific languages they speak. Language is essential to our complex social life, revolving as it does around institutions that are transmitted by language and operated by oratory. The evolution of language as a human capacity, and of languages themselves, are subjects of a large and growing literature. Many important and controversial issues are under examination including the roles of cultural and genetic evolution in the process and the role of general purpose versus language specific innate cognitive resources. Culture itself evolves by processes that are something like the evolution of genes, but which are different in many important details. In the case of language, the cultural evolutionary processes by which



languages change over time are tolerably well understood from the work of socio-linguists (Labov 1994, Labov 2001) and historical linguists (Deutscher 2005). The application of formal phylogenetic methods borrowed from evolutionary biology to the reconstruction of language evolution is an active area of research (Gray *et al.* 2009, Pagel 2009). We have reasonable general models of cultural evolution (Henrich & McElreath 2008). We have good models of the coevolutionary process (Richerson & Boyd 1989, Feldman & Laland 1996).

The coevolutionary approach to the evolution of language was first articulated by Pinker & Bloom (1990). They imagine that the first step in the evolution of human language would be a rudimentary culturally transmitted set of signals. If having such signals were adaptively advantageous, selection might fall in genes to expand the capacity to acquire such signals. So long as a higher capacity cultural communication system was favored, cognitive modifications to more efficiently acquire explicitly linguistic features like symbolic words and grammar would be favored as the system passed some threshold of complexity. Eventually, languages with a rather large vocabulary and complex syntax and/or morphology became cognitively possible. Coevolution assumes that some relatively easy and gradual path was available such that the evolution of language could proceed from simple vocal and gestural communications to human language by some combination of small cultural and innate steps, at least after some key cognitive precursors had evolved (Origgi & Sperber 2000). See Donald (1991), Deacon (1997), Tomasello (2008), and Progovac (this volume) on how language might have evolved gradually.

Pinker (2003) continues to argue that humans were equipped by the coevolutionary process with specialized innate mechanisms to manage language acquisition, production, and comprehension. Others have argued that more general cognitive resources, perhaps especially resources shared by other domains of culture, can underpin language. We have formal models of how language specific features like compositionality might evolve by cultural evolution by languages adapting to be learnable using general cognitive resources (de Boer 2000, Munroe & Cangelosi 2002, Smith & Kirby 2008). Steels (2009) has simulated how language might be invented using sufficiently powerful general cognitive resources using laboratory robots. Briscoe (2009) argues that even if general cognitive resources are sufficient to initiate simple languages, coevolution would have produced at least some language specific biases and constraints to make language more efficiently learnable. Of course, some genetic changes must have accompanied the evolution of language since even chimpanzees and bonobos when raised in a linguistic environment develop, at best, a rudimentary form of language (Savage-Rumbaugh & Lewin 1994). Tomasello (2008) emphasizes the idea of a cognitive complex of shared attention, collaborative activities, social motivation and cultural evolution that is important for language *and* technical and social skills. Bloom (2000) emphasized the cognitive strategies used to learn words. Dehaene's (2009) interesting work on reading shows how visual circuits evolved to process normal visual stimuli can be 'recycled' to transmit linguistic information in the visual mode, providing a possible

model for earlier coevolutionary events. Nettle (2007) raises the possibility that this sort of coevolution still goes on. Subtle differences in innate capacities may have coevolved with different language families; for example, populations with a long history of using tone to make linguistic distinctions may find it slightly easier to learn and use tones than populations not so exposed (Dediu & Ladd 2007). Good evidence to this effect would suggest that the coevolutionary process indeed affects language evolution. Thus, while a consensus exists that human language evolved by a coevolutionary scenario, evolutionary linguists differ greatly on the details.

This bare-bones account leaves many unanswered questions. Two seem fundamental to us. First, why is human language unique? Not only primates but also parrots and songbirds have preadaptations for vocal communication and vocal imitation (Baptista & Trail 1992, Pepperberg 2000). Human language is widely counted as our most spectacular adaptation, the very adaptation that made us human, and the adaptation that constitutes the latest 'major transition of life' (Maynard Smith & Szathmáry 1995). Maynard Smith & Szathmáry's other major transitions happened long ago; why was this one so tardy? Many species would seem to have rudimentary communication systems that could fall under the influence of the coevolutionary mechanism outlined above. Under what scenario might humans, but not other species, come under selection for an advanced inter-individual communication system?

The functional hallmark of human language is to combine a large vocabulary of meaningful words into utterances using syntactic rules that convey much information about how the string of words in an utterance modify each other's meanings. How might evolutionary processes favor the evolution of a high information volume communication system in humans? One possible answer is that humans were the first to acquire some sort of cognitive breakthrough. For example, Sperber (2000) is concerned with whether 'metarepresentation' (the ability to represent the thoughts of others) is a precondition for the evolution of language and Donald (2001) with the issue of whether human cultural capacities had to be fairly advanced before language could arise. In contrast, we suggest that syntax and semantics are the easy part of the evolution of language. The hard part is to figure out how humans could make use of language. Less provocatively, given innate cognitive adaptations of some kind were necessary for language, to use language, hearers must trust speakers. If they did not, they would not listen, and language would collapse. Grice (1975: 45) noted that to function conversation had to conform to a cooperative principle. But evolutionary biology teaches us that trust between individuals evolves with difficulty. Hence, the difficulty from the evolutionary perspective is how trust can evolve. If trust evolves, the cognitive bases of complex communication might evolve without serious impediment. The problem of cooperation is central to a number of accounts of the evolution human language (e.g., Hurford 2007, Tomasello 2008).

Second, how can we account for the large role of culture in language? Noam Chomsky has recently advocated a minimalist approach to the innate components of language (Chomsky 1995, 2005, Hauser *et al.* 2002). Minimalists themselves debate

about exactly what is innate, what is perhaps innate but not specific to language, and what can be off-loaded to the cultural system (e.g., Arsenijević & Hinzen, this volume). Generative grammarians who pursued the idea that surface diversity of grammars could be rigorously tied to a parsimonious set of principles and parameters seem not to have succeeded (Newmeyer 2005). Agreeing with this assessment, sociolinguists and historical linguists propose mechanisms, based on observations about how language actually changes generation by generation, that seem to account for how a vast diversity of languages can evolve culturally (Guy 1996, Deutscher 2005). Whatever is innate is very deep and hardly constrains the design space of syntax and lexicon (Progovac, this volume).

We can imagine that language learning and subsequent communication would be more efficient if more of it was innate. This is seemingly the logic of the much mooted massive modularity hypothesis for cognitive architecture generally (Tooby & Cosmides 1989, Sterelny 2003). For example, we could imagine a communication system that is largely specified innately (Sampson 2002). Such a system might superficially resemble a family of languages like the Romance Languages. Most of the grammar and much of the vocabulary would be quite similar across all the world's languages, yet a 'Castilian' child adopted by 'Catalans' might have considerable difficulty learning 'Catalan' because of having innate adaptations to speak 'Castilian'. Or perhaps everyone would just innately speak 'Catalan', but with minor culturally determined 'Valencian' and 'Barcelonan' dialects. This scenario is clearly counterfactual. Languages seem to be much more culturally diverse than they need to be for communicative efficiency. Students of the structural variation in human languages keep discovering structural principles as the number of well-studied languages grows to the point of questioning whether there are any language universals at all (Evans & Levinson 2009). Indeed, their balkanization into thousands of mutually unintelligible languages and tens of thousands mutually difficult to understand dialects is odd if selection fell only on communicative efficiency. Wouldn't communicative efficiency be maximized if we innately spoke a common regular language like Esperanto? We need to ask if language *variation* is somehow adaptive.

2. Why Possibly Language is Restricted to Humans

Language is not the only rich communication system in nature. The cells in our body use nerves and hormones to coordinate our exceedingly complex development, physiology and behavior. For example, the development of complex organisms proceeds by intercellular signaling such that each cell eventually matures in the type appropriate for the tissue it finds itself in. The famous FOXP2 gene codes for a regulatory protein active in the development of all vertebrates. The common human variant differs at two amino acids from that in chimpanzees and a particular rare variant causes a specific language impairment in one well-studied family. However,

FOXP2 is expressed in many tissues during development in humans. Preliminary broad scale scans suggest that it may have hundreds of targets in a variety of tissues (Fisher & Scharff 2009). If so, one might imagine that genes exhibit the property of compositionality. FOXP2 is like a 'word' with a particular meaning that can participate in many developmental 'sentences'. We are not aware of any careful analysis intercellular communication systems for formal analogies to language, but as we learn more about how these systems work, they might be grist for comparative analysis. Interestingly, biologists have described many mechanisms by which rich internal communication systems are 'policed' to ensure a community of interest, safeguarding the basis of communication (Frank 2003). Such policing is necessary because pressure from deceptive entities, like cancer cells, to reproduce at the expense of the collective always exists.

The mathematical theory of animal communication was pioneered by John Maynard Smith (1976, 1994) and has recently been applied to human language by Lachman *et al.* (2001) and Lachmann & Bergstrom (2001, 2004). The basic problem is that individuals do not normally have enough commonality of interests to make honest communication possible. The relationship between individuals is normally competitive, and any communication thus tends to be self-interested. However, this self-interestedness means that recipients of communications cannot trust the talk of communicators, so free communication does not evolve. Thus, animal communication is normally extremely impoverished. Animal communications are costly signals, cases in which deceptive signals can be punished cheaply, or cases in which the 'communication' is an unmodifiable index of some attribute, as size is an index of strength. Peacocks' tails and the red deer stag's adaptations for male-male combat are two stock examples of costly signals. These features advertise the size and health status of males, the quality of their genes, and their fighting prowess to others in the vicinity in order to attract females and intimidate competing males. These signals are trustworthy indicators of male quality because only large, healthy males can carry a large display of gaudy feathers or develop the muscles and antlers to be competitive in fights between males. A male that produced deceptively large but weak antlers would risk injury if he had his bluff called by males with well-constructed antlers. A population might start with cheap, accurate signals of genetic quality or fighting prowess, but such communication will be undermined by mutant males that use resources to fake the signal, resulting in an arms race that ends up with an expensive unfakable signal. At an evolutionary equilibrium, the signal will be so costly that inferior males simply have insufficient resources to generate a fake signal of quality. Such a system has such a high overhead that it can produce only a handful of critical messages. Maynard Smith & Harper (2003) discuss some situations in which signals do not have to be costly subject to punishment. The most important one relevant to language is that in some situations individuals have no conflicts of interest. For example a foreign motorist might ask us to explain a traffic rule. We would have an interest in providing the correct answer, at least if the foreigner is driving on the same road, because having the correct answer will make her less likely to hit us.

Lachmann & Bergstrom show that a combinatorial communication system that relies on rules to interpret a sentence composed of words is especially vulnerable to deceptive messages and is therefore requires considerable cooperation to evolve. The value of a combinatorial communication system is that it permits limitless flexibility in the construction of messages using a finite number of words, but deceivers can use this flexibility to compose artful manipulative messages that recipients will interpret to the advantage of the signaler but to their own detriment. Merely policing the meanings of words and grammatical rules will not prevent lying. Thus, the theory tells us that rich combinatorial language-like systems evolve under a special handicap. This perhaps helps explain why language-like rich communication systems are of very restricted occurrence.

Human language is part of the extraordinary cooperation of humans with distantly related or unrelated people. The philosopher of language Paul Grice was the first person to note the centrality of cooperation in language, and many evolutionary linguists have concurred (Grice 1975; see also Sperber & Wilson 1995, Dessalles 1998, Knight 1998, Csibra & Gergely 2006, and Hurford 2007). Cooperation in language exists at two levels (Hurford 2007). First speakers must agree on common definitions of words and use the same grammatical rules if any communication is to take place at all. Second, language usage would collapse (or never arise in the first place) if speakers did not generally provide useful information to hearers, as the mathematical theory suggests. We take it that coordination on the meaning of words and grammatical rules is an easier evolutionary problem than the problem of maintaining high levels of truthfulness in the face of self-serving temptations. Because humans cooperate in large groups of distantly related and unrelated individuals, we both have a use for language — to organize our social life — and enough commonality of interest to support a rich, cheap, and trustworthy communication system (Nettle 2006, Tomasello 2008). We also police the system — telling a lie is a sin (Scott-Phillips 2008).

A number of evolutionary hypotheses are on the table to explain this cooperation (Richerson *et al.* 2003, Krebs 2008). One of these is the Tribal Social Instincts hypothesis (Richerson & Boyd 1999), which is a modernization of a hypothesis first proposed by Darwin (1874) in the *Descent of Man*. It proposes that human cooperation arose because human *cultural* variation is especially susceptible to selection at the level of the group. The ancestral groups that were relevant during the evolution of our social psychology were tribes, ethnolinguistic units ranging in size from a few hundred to a few thousand people. Normally, selection is strongest at the level of individuals, leading to competition between individuals for reproductive success. Groups of individuals can fall under strong enough selection to lead to within group cooperation, but the conditions are fairly stringent except when groups are small or closely related. Kin assortment leads to reduced genetic variation within groups and exaggerated variation between them, and group selection requires persistent genetic variation at the group level to work. The reasons that culture is unusually susceptible to group selection on a much larger scale than genetic kin groups are outlined in Richerson & Boyd (2005: 203–213) and more formally by

Henrich (2004). The linguist reader should be warned that the evolution of cooperation literature is bedeviled by terminological claims masquerading as scientific ones. Recent examples include West *et al.* (2007) and Gardner & Grafen (2009).

The basic idea is that culture much more easily than genes preserves variation between large groups of unrelated or distantly related individuals. Culture evolves more rapidly than genes because culture is modified by learned innovations not just random mutation and because we can actively choose superior variants either by direct experimentation with variants or by rules of thumb like imitating the successful or prestigious. Preserving variation between groups requires that variation between groups has to evolve fast enough to mitigate the blending effects of migration. In genetic evolution, selection and drift are generally not able to maintain much variation between neighboring groups whereas cultural processes can. Bell *et al.* (2009) used the World Values Survey to estimate cultural variation between neighboring nations and compared these estimates to published estimates of genetic variation for the same nations. Mean cultural differences are more than ten times greater than genetic differences, and the cultural differences are probably underestimated. Many important differences between groups are institutions maintained by social sanctions (Herrmann *et al.* 2008). If punishment keeps deviants rare, the differences between neighboring societies can be virtually categorical. We will shortly consider a linguistic mechanism that limits mixing between groups, helping to preserve between group variation.

Innate elements of our social psychology — Darwin argued that sympathy and patriotism were among our ‘social instincts’ — would have evolved by gene-culture coevolution following the same logic outlined above for the language faculty. Language would have been an important element of the evolution of cooperation. Language is obviously a general purpose communication system that today we use to talk about practically everything. For the purpose of formulating hypotheses about the intertwined evolution of language and cooperation, we need to imagine what the main function(s) of protolanguage were near the beginning of the co-evolutionary sequence that eventually gave rise to our advanced capacity for language. To get an impression of what mimetic pre-linguistic but otherwise highly imitative hominins might have been able to do without language, Donald (1991) reviewed the literature on 19th century people deaf from birth (so-called then ‘deaf-mutes’). Deaf-from-birth people led surprisingly normal lives even when they acquired no language skills beyond simple ‘home signs’ they invented to communicate with family members. Most of them learned skills necessary to support themselves, typically a manual trade or farming, and some became prosperous. Many married and otherwise had relatively normal social lives. This evidence suggests, Donald argues, that humans might well have had a fairly advanced cultural system *before* the capacity for language evolved. Thus, cultural group selection might have selected for a measure of extra-familial altruism before the evolution of language even began.

However, we think it unlikely that social systems of the complexity that living hunter-gatherers operate could have functioned without language (see Dunbar 1996

for a slightly different version of this argument). The social life of even the simplest known hunter-gatherer societies, such as the San peoples of the Kalahari and the Shoshone of the North American Great Basin, was regulated by institutions, commonly known rules governing social behavior (Maryanski & Turner 1992). For example, the famous !Kung (Ju/'hoansi) San peoples have a complex tripartite kinship system that in effect makes everyone at least a fictive kin to everyone else, even if no genea-logical connection is known (Lee 1986). They also have a ceremonial gift exchange system that cements ties of friendship with people living in distant camps (Wiessner 2002). A large number of the gift relationships are with distantly related people, especially on the part of successful hunters and their wives. Even these comparatively simple institutions are encoded, transmitted, and reinforced linguistically through stories, gossip, complaining and shaming (Wiessner 2005). In many cases, hunter-gatherer social institutions were not at all simple. The marriage systems of the societies in the Australian central desert were very elaborate, for example (Yengoyan 1968). One might imagine that the first steps toward human cooperation in large groups might have taken place before language, but it is hard to see complex institutions arising and being maintained across a large group without it.

The general proposition that human intelligence evolved for its social functions is sometimes called the social intelligence or Machiavellian intelligence hypothesis (Dunbar 1996, Whiten & Byrne 1997). It is often contrasted with an ecological intelligence hypothesis. We think that the social intelligence hypothesis as usually stated does not give sufficient attention to the fact that hunter-gatherer *subsistence* was an intensely *social* enterprise (Steward 1955). In humans, social intelligence is fundamental to our ecological adaptation. The human hunting and gathering adaptation depended substantially upon cooperative big game hunting, especially during the late Pleistocene (Stiner 2002). Hunting probably provided the nutrients necessary to grow and sustain our very expensive brain (Aiello & Wheeler 1995, Kaplan *et al.* 2000). Many of the skills involved in hunting could perhaps have been learned by alinguistic imitation — all those skills for which a picture is worth a thousand words. However, at least one skill, tracking, is practiced in living hunter-gatherers as a sophisticated collective hypothesis testing enterprise in which verbal discussion is essential (see also Liebenberg 1990, Guthrie 2005). Trackers need to have natural-historical knowledge that often outruns that of the modern naturalists who have interacted with them (Blurton-Jones & Konner 1976) and would no doubt be hard to transmit without language.

The evolution of human intelligence might well have been driven directly by recent climate deterioration. Some theoretical and empirical evidence supports the idea that the evolution of complex, cumulatively improvable culture, including languages, was driven directly by increasingly variable environments over the last few million years (Calvin 2002, Richerson *et al.* 2005). Simple evolutionary models of culture suggest that the main adaptive advantage of a costly system of social learning is adaptation to environments with rapid, high amplitude variation (Boyd & Richerson 1985). If environmental variation is modest or if change is slow, genetic

evolution tracks changes well enough. If it is very rapid, then adaptation is via mechanisms of phenotypic flexibility like individual learning and important parts of the immune system. Combining individual phenotypic flexibility with the inheritance of acquired variation by social learning is adaptive in environments with high variability but intermediate rates of change. Culture can economize on learning by creating transmitted adaptations to environments that persist for a generation to some tens or even hundreds of generations. Work on ice and ocean cores has shown that the last ice age had the sort of high amplitude millennial and sub-millennial scale variation climate variation that the models predict would favor culture (Alley 2000). A recent ocean core suggests that the amount of millennial and sub-millennial scale variation has increased over the last four ice ages (Martrat *et al.* 2007). If the symbolic artifacts recovered by paleoanthropologists — scarcer and simple before 50,000 year ago, more numerous and more sophisticated after that date — are indicative of the emergence or improvement of languages, they may have evolved in response to the demands of the hypervariable climate of the last ice age. Coincidentally or not the hypervariable part of the last ice age started about 70,000 years ago, not long before the paleoanthropological evidence suggests that human symbolic capacities and other indications of behavior likely to be related to language appeared in the record, and shortly before modern humans spread out of Africa (Richerson *et al.* 2009). As far as is currently known, the particular pattern of climate variability of the Plio-Pleistocene ice ages is unique and is thus a candidate to help explain why the human ‘major transition’ occurred so recently.

3. Why is Language Weakly Constrained by Genes?

The number and diversity of human languages is stunning, akin to the species diversity of rain forest trees and coral reef fishes (Nettle 1999). The total number of living languages in the world is currently about 7,000 (<http://www.ethnologue.com>), about 1,000 of which are spoken on New Guinea. Unlike species that typically differ in functionally important ways, languages are largely functionally equivalent.

Several authors have suggested that the function of language and similar symbolic differences is to mark the boundaries of social groups (Labov 1973, Nettle & Dunbar 1997, Livingstone & Fyfe 1999, Nettle 1999, and Livingstone 2002). They serve to identify those who are ‘like us’ and those who belong to other groups. Language differences function to *limit* communication and hence the spread of ideas from one community to another. People from other groups are liable to tell you self-serving lies. They are also likely to tell you things that are useless in the physical and social ecology in which you live. Human cultures are ecologically a lot like species. They typically have different social institutions and often different ways of making a living (Barth 1969). Imitating people from a different culture may often be a bad thing to do (Gil-White 2005). Language diversity perhaps limits communication adaptively.

Mathematical models support this line of reasoning. Boyd & Richerson (1987) studied a cultural evolutionary model in which two populations lived in different environments. A different value of a quantitative adaptive character was optimal in each environment and there was a generic neutral marker character, also quantitative. (Quantitative characters are behaviors that can be measured on a continuous scale, such as the location of a vowel in formant space). Individuals migrated between the two populations, tending to homogenize them at some intermediate value of the adaptive character not well adapted to either environment. Counteracting mixing, juveniles were assumed to have a tendency to adopt the value of the adaptive character from people whose value of the neutral marker, say their dialect, resembled theirs. They also prefer to imitate people who are successful. In the model, the marker characters in the two populations diverged, generating a correlation between the marker and the adaptive trait. At equilibrium, the mean value of the adaptive trait was at the optimum in both environments. The preference for imitating people like you with regard to a neutral marker trait in the presence of a strong correlation between adaptive and marker characters set up an adaptive barrier limiting the flow of wrong ideas from the other environment even in the face of rather strong physical migration.

McElreath *et al.* (2003) studied a conceptually similar model but this time using discrete characters. They also modeled the environment as a social game of coordination rather than a different physical environment. Games of coordination are ones in which high payoffs depend upon matching the behavior of others. Languages are a massive game of coordination. Unless our grammar and lexicon at least roughly match those with whom we wish to communicate, we will fail. Once again migration tends to homogenize the populations but a correlation arises between the neutral marker characters and the move in the game of coordination. Eventually people in the two populations usually play with partners that correctly match their coordination move. Because language can evolve differences so rapidly, it can evolve to calibrate our discrimination against outsiders quite sensitively. I may perfectly well understand someone whose dialect differs only modestly from mine, but I may still distrust them. On the other hand, someone speaking a strange dialect is offering me something that I can judge independently to be highly useful, I might adopt it despite a general suspicion of such folks. Sociolinguists tell us that we make many social decisions based on subtle linguistic differences. Those who study the diffusion of innovations tell us that we can overcome linguistic barriers to the diffusion of ideas and techniques if we are sufficiently motivated. The models are very crude by comparison, but they lend credence to the adaptive importance of linguistic diversity but also to the flexibility of linguistic boundaries. Efferson *et al.* (2008) verified that symbolic markers could evolve in laboratory microsocieties.

Interestingly, in McElreath *et al.*'s (2003) model, symbolic differentiation cannot arise in the first instance to mark cooperators. (See Nettle & Dunbar (1997) for a model with different results.) The reason is that carrying a mark that identifies an individual as a cooperator favors the evolution of selfish non-cooperators who carry

the mark and victimize true cooperators. Games of coordination and ordinary adaptive differences do not contain a dilemma of cooperation and are not vulnerable to this problem. What symbolic differences, first among them linguistic differences, will do is inhibit communication between groups, tending to preserve variation between groups. Selection between such groups can then lead to ingroup cooperation and distrust of outgroups (Richerson & Boyd 2005).

These model results are in rough accord with the literature on ethnicity (LeVine & Campbell 1972). People speaking different languages may not normally communicate much, but, unlike biological species, they are not completely informationally isolated from one another. Ethnographic data from small-scale societies suggest that linguistic and other symbolic boundaries often mark the limits of trust and cooperation. The role of ethnicity in conflict in modern societies is well known (e.g., Horowitz 2001).

The role of language as a symbolic marker of group boundaries has been well studied by sociolinguists (Labov 1980, 2001). Labov and other sociolinguists discovered that subtle phonological changes grow up rapidly wherever social fault lines arise. For example, on Martha's Vineyard, a rural island off the coast of Massachusetts, the influx of summer tourists caused Vineyarders' speech to diverge detectably from the standard New England dialect. People seem to condition their behavior on the dialects that others speak. It is not hard to project the sociolinguistic mechanisms that cause small-scale generation to generation changes in languages to the multigeneration scale on which new dialects, new languages, and eventually new language families evolve (Nettle 1999, Deutscher 2005). Among the fields of language change that strike us as well studied include grammaticalization, the process by which conventional lexical constructions come to have syntactic functions (Hopper & Traugott 2003) and the way in which languages in contact influence each other (Thomason 2001).

4. Conclusion

The theory of gene-culture coevolution has provided a useful framework for analyzing the evolution of language. Indeed, we are not aware of any contemporary students of language evolution who do not subscribe to some form of coevolutionary argument. Evolutionary linguists do differ about the division of labor between genes and culture that they propose. Some authors such as Tomasello (2008) and Kirby *et al.* (2009) posit a large role for culture in adapting language to pre-linguistic cognitive capacities or ones shared with other aspects of culture. Others, for example Pinker (2003), argue for much language specific innate cognitive adaptation. Evolutionists could contribute to this debate if it were clear what the design constraints on cognitive architecture are. The idea that specialized cognitive architecture is highly efficient is appealing, but the relatively general heuristics like joint attention that make cultural transmission efficient are impressive as well. The detailed answer

to the division of labor question is, we think, largely a matter for neurobiologists to unravel. Evolutionary considerations can provide a theory for the level of trust and cooperation necessary to make cheap, accurate, and abundant communication between humans possible and an explanation for why at least some cultural variation remains in language. In conjunction with data from paleoanthropology, paleoclimatology, and paleoecology we can produce hypotheses about when language probably evolved and why it evolved only in the human lineage. Without doubt, all of these are very difficult questions. We do not flatter ourselves that the specific proposals here will survive challenges of new data, for example data on the history of the genes that underpin language. We are more confident that the form of the coevolutionary analysis is correct.

References

- Aiello, Leslie C. & Peter Wheeler. 1995. The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology* 36, 199–221.
- Alley, Richard B. 2000. *The Two-Mile Time Machine: Ice Cores, Abrupt Climate Change, and Our Future*. Princeton, NJ: Princeton University Press.
- Arsenijević, Boban & Wolfram Hinzen. This volume. Recursion as a human universal and as a primitive.
- Baptista, Luis F. & Pepper W. Trail, 1992. The role of song in the evolution of passerine birds. *Systematic Biology* 41, 242–247.
- Barth, Fredrik. 1969. *Ethnic Groups and Boundaries: The Social Organization of Culture Difference*. Boston, MA: Little Brown & Company.
- Bell, Adrian V., Peter J. Richerson & Richard McElreath. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human pro-sociality. *Proceedings of the National Academy of Sciences USA* 106, 17671–17674.
- Bloom, Paul. 2000. *How Children Learn the Meanings of Words*. Cambridge, MA: MIT Press.
- Blurton-Jones, Nicholas & Melvin Konner. 1976. !Kung knowledge of animal behavior. In Richard B. Lee & Irven DeVore (eds.), *Kalahari Hunter-Gatherers: Studies of the !Kung San and Their Neighbors*, 325–348. Cambridge: Cambridge University Press.
- de Boer, Bart. 2000. Self-organization in vowel systems. *Journal of Phonetics* 28, 441–465.
- Boyd, Robert & Peter J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago, IL: University of Chicago Press.
- Boyd, Robert & Peter J. Richerson. 1987. The evolution of ethnic markers. *Cultural Anthropology* 2, 65–79.

- Boyd, Robert & Peter J. Richerson. 2005. *The Origin and Evolution of Cultures*. Oxford: Oxford University Press.
- Briscoe, Ted. 2009. What can formal or computational models tell us about how (much) language shaped the brain? In Derek Bickerton & Erös Szathámry (eds.), *Biological Foundations and the Origin of Syntax*, 369–382. Cambridge, MA: MIT Press.
- Calvin, William H. 2002. *A Brain for All Seasons: Human Evolution and Abrupt Climate Change*. Chicago, IL: University of Chicago Press.
- Chomsky, Noam. 1995. *The Minimalist Program*. Cambridge MA: MIT Press.
- Chomsky, Noam. 2005. Three factors in Language Design. *Linguistic Inquiry* 36, 1–22.
- Csibra, Gergely, & György Gergely. 2006. Social learning and social cognition: The case for pedagogy. In Yuko Munakata & Mark H. Johnson (eds.), *Processes of Change in the Brain and Cognitive Development. Attention and Performance, XXI*, 249–274. Oxford: Oxford University Press.
- Darwin, Charles M.A. 1874. *The Descent of Man, and Selection in Relation to Sex*. New edn., revised and augmented. New York: Hurst & Company.
- Deacon, Terrence W. 1997. *The Symbolic Species: The Co-Evolution of Language and the Brain*. New York: Norton.
- Dediu, Dan & D. Robert Ladd. 2007. Linguistic tone is related to the population frequency of the adaptive haplogroups of two brain size genes, *ASPM* and *Microcephalin*. *Proceedings of the National Academy Sciences USA* 104, 10944–10949.
- Dehaene, Stanislas. 2009. *Reading in the Brain: The Science and Evolution of a Human Invention*. New York: Viking.
- Dessalles, Jean-Louis. 1998. Altruism, status, and the origin of relevance. In James R. Hurford, Michael Studdert-Kennedy & Chris Knight (eds.), *Approaches to the Evolution of Language: Social and Cognitive Bases*, 130–149. Cambridge: Cambridge University Press.
- Deutscher, Guy. 2005. *The Unfolding of Language: An Evolutionary Tour of Mankind's Greatest Invention*. New York: Henry Holt.
- Donald, Merlin. 1991. *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition*. Cambridge, MA: Harvard University Press.
- Donald, Merlin. 2001. *A Mind So Rare: The Evolution of Human Consciousness*. New York: W.W. Norton.
- Dunbar, Robin I. M. 1996. *Grooming, Gossip and the Evolution of Language*. Cambridge MA: Harvard University Press.
- Efferson, Charles, Rafael Lalive & Ernst Fehr. 2008. The coevolution of cultural groups and ingroup favoritism. *Science* 321, 1844–1849.
- Evans, Nicholas & Stephen C. Levinson, 2009. The myth of language universals: Language diversity and its importance for cognitive science. *Behavior and Brain Sciences* 32, 429–492.
- Feldman, Marc W. & Kevin N. Laland. 1996. Gene-culture coevolutionary theory. *Trends in Ecology and Evolution* 11, 453–457.

- Fisher, Simon E. & Constance Scharff. 2009. FOXP2 as a molecular window into speech and language. *Trends in Genetics* 25, 166–177.
- Frank, Steven A. 2003. Perspective: Repression of competition and the evolution of cooperation. *Evolution* 57, 693–705.
- Gardner, Andy & Alan Grafen. 2009. Capturing the superorganism: A formal theory of group adaptation. *Journal of Evolutionary Biology* 22, 659–671.
- Gil-White, Francisco. 2005. Is ethnocentrism adaptive? An ethnographic analysis. Unpublished manuscript, University of Pennsylvania, Philadelphia. [<http://www.hirhome.com/academic/Ethnocentrism.pdf>.]
- Gray, Russell D., Alexei J. Drummond & Simon J. Greenhill. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* 323, 479–483.
- Grice, H. Paul. 1975. Logic and conversation. In Peter Cole & James Morgan (eds.), *Syntax and Semantics*, vol. 3: *Speech Acts*, 41–58. London: Academic Press.
- Guthrie, R. Dale. 2005. *The Nature of Paleolithic Art*. Chicago, IL: Chicago University Press.
- Guy, Gregory R. 1996. *Towards a Social Science of Language: Papers in Honor of William Labov*. Amsterdam: John Benjamins.
- Hauser, Marc D., Noam Chomsky & W. Tecumseh Fitch. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298, 1569–1579.
- Henrich, Joe & Richard McElreath. 2008. Dual inheritance theory: The evolution of human cultural capacities and cultural evolution. In Robin Dunbar & Louise Barrett (eds.), *Oxford Handbook of Evolutionary Psychology*, 571–585. Oxford: Oxford University Press.
- Henrich, Joseph. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. A target article with commentary. *Journal of Economic Behavior and Organization* 53, 3–143.
- Herrmann, Benedikt, Christian Thöni & Simon Gächter. 2008. Antisocial punishment across societies. *Science* 319, 1362–1367.
- Hopper, Paul J. & Elizabeth Closs Traugott. 2003. *Grammaticalization*. Cambridge: Cambridge University Press.
- Horowitz, Donald L. 2001. *The Deadly Ethnic Riot*. Berkeley, CA: University of California Press.
- Hurford, James R. 2007. *The Origins of Meaning*. Oxford: Oxford University Press.
- Kaplan, Hillard, Kim Hill, Jane Lancaster & A. Magdalena Hurtado. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 9, 156–185.
- Kirby, Simon, Morton H. Christiansen & Nick Chater. 2009. Syntax as an adaptation to the learner. In Derek Bickerton & Eros Szathmary (eds.), *Biological Foundations and the Evolution of Syntax*, 325–343. Cambridge, MA: MIT.
- Knight, Chris. 1998. Ritual/speech coevolution: A solution to the problem of deception. In James R. Hurford, Michael Studdert-Kennedy & Chris Knight (eds.), *Approaches to the Evolution of Language: Social and Cognitive Bases*, 68–91.

- Cambridge: Cambridge University Press.
- Krebs, Dennis L. 2008. Morality: An evolutionary account. *Perspectives on Psychological Science* 3, 149–172.
- Labov, William. 1973. *Sociolinguistic Patterns*. Philadelphia, PA: University of Pennsylvania Press.
- Labov, William. 1980. *Locating Language in Time and Space*. New York: Academic Press.
- Labov, William. 1994. *Internal Factors — Principles of Linguistic Change*, vol. I. Malden, MA: Blackwell.
- Labov, William. 2001. *Social Factors — Principles of Linguistic Change*, vol. II. Malden, MA: Blackwell.
- Lachmann, Michael & Carl T. Bergstrom. 2004. The disadvantage of combinatorial communication. *Proceedings of the Royal Society of London B* 271, 2337–2343.
- Lachmann, Michael, Szabolcs Szamado & Carl T. Bergstrom. 2001. Cost and conflict in animal signals and human language. *Proceedings National Academy of Sciences USA* 98, 13189–13194.
- Lee, Richard. 1986. !Kung kin terms, the name relationship and the process of discovery. In Megan Biesele, Robert Gordon & Richard Lee (eds.), *The Past and Future of !Kung Ethnography: Critical Reflections and Symbolic Perspectives — Essays in Honour of Lorna Marshall*, 77–102. Hamburg: Helmut Buske Verlag.
- LeVine, Robert & Donald T. Campbell. 1972. *Ethnocentrism: Theories of Conflict, Ethnic Attitudes, and Group Behavior*. New York: Wiley.
- Liebenberg, L. 1990. *The Art of Tracking: The Origin of Science*. Cape Town: David Phillip.
- Livingstone, Daniel. 2002. The evolution of dialect diversity. In Angelo Cangelosi & Domenico Parisi (eds.), *Simulating the Evolution of Language*, 99–117. London: Springer.
- Livingstone, Daniel & Colin Fyfe. 1999. Modeling the evolution of linguistic diversity. In Dario Floreano, Jean Daniel Nicoud & Francesco Monada (eds.), *Proceedings of the 5th European Conference in Artificial Life: ECAL '99*, 704–708. Lausanne: Springer.
- Martrat, Belen, Joan O. Grimalt, Nicholas J. Shackleton, Lucia de Abreu, Manuel A. Hutterli & Thomas F. Stocker. 2007. Four climate cycles of recurring deep and surface water destabilizations on the Iberian margin. *Science* 317, 502–507.
- Maryanski, Alexandra & Jonathan H. Turner. 1992. *The Social Cage: Human Nature and the Evolution of Society*. Stanford, CA: Stanford University Press.
- Maynard Smith, John. 1976. Sexual selection and the handicap principle. *Journal of Theoretical Biology* 57, 239–242.
- Maynard Smith, John. 1994. Must reliable signals always be costly? *Animal Behaviour* 47, 1115–1120.
- Maynard Smith, John & David Harper. 2003. *Animal Signals*. Oxford: Oxford University Press.
- Maynard Smith, John & Eörs Szathmáry. 1995. *The Major Transitions in Evolution*.

- Oxford: W.H. Freeman/Spectrum.
- McElreath, Richard, Robert Boyd & Peter J. Richerson. 2003. Shared norms and the evolution of ethnic markers. *Current Anthropology* 44, 122–129.
- Munroe, Steve & Angelo Cangelosi. 2002. Learning and the evolution of language. *Artificial Life* 8, 311–339.
- Nettle, Daniel & Robin I. M. Dunbar. 1997. Social markers and the evolution of reciprocal exchange. *Current Anthropology* 38, 93–99.
- Nettle, Daniel. 1999. *Linguistic Diversity*. Oxford: Oxford University Press.
- Nettle, Daniel. 2006. Language: Costs and benefits of a specialized system for social information transmission. In Jonathan C. K. Wells, Simon Strickland & Kevin Laland (eds.), *Social Information Transmission and Human Biology*, 137–152. London: Taylor & Francis.
- Nettle, Daniel. 2007. Languages and genes: A new perspective on the origins of human cultural diversity. *Proceedings National Academy of Sciences USA* 104, 10755–10756.
- Newmeyer, Fredrick J. 2005. *Possible and Probable Languages: A Generative Perspective on Linguistic Typology*. Oxford: Oxford University Press.
- Origg, Gloria & Dan Sperber. 2000. Evolution, communication and the proper function of language. In Peter Carruthers & Andrew Chamberlin (eds.), *Evolution and the Human Mind: Modularity, Language, and Meta-Cognition*, 140–169. Cambridge: Cambridge University Press.
- Pagel, Mark. 2009. Human language as a culturally transmitted replicator. *Nature Reviews Genetics* 10, 405–415.
- Pepperberg, Irene M. 2000. *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots*. Cambridge, MA: Harvard University Press.
- Pinker, Steven. 2003. Language as an adaptation to the cognitive niche. In Morten H. Christiansen & Simon Kirby (eds.), *Language Evolution*, 16–37. Oxford: Oxford University Press.
- Pinker, Steven & Paul Bloom. 1990. Natural language and natural selection. *Behavioral and Brain Sciences* 13, 707–784.
- Progovac, Ljiljana. This volume. Syntax: Its evolution and its representation in the brain.
- Richerson, Peter J. & Robert Boyd. 1989. The role of evolved predispositions in cultural evolution: Or sociobiology meets Pascal's Wager. *Ethology and Sociobiology* 10, 195–219.
- Richerson, Peter J. & Robert Boyd. 1999. Complex societies — The evolutionary origins of a crude superorganism. *Human Nature* 10, 253–289.
- Richerson, Peter J., Robert Boyd & Joseph Henrich. 2003. Cultural evolution of human cooperation. In Peter Hammerstein (ed.), *Genetic and Cultural Evolution of Cooperation*, 357–388. Cambridge, MA: MIT Press.
- Richerson, Peter J., Robert L. Bettinger & Robert Boyd. 2005. Evolution on a restless planet: Were environmental variability and environmental change major drivers of human evolution? In Franz M. Wuketits & Francisco J. Ayala (eds.),

- Handbook of Evolution: Evolution of Living Systems (Including Hominids)*, 223–242. Weinheim: Wiley-VCH.
- Richerson, Peter J. & Robert Boyd. 2005. *Not By Genes Alone: How Culture Transformed Human Evolution*. Chicago, IL: University of Chicago Press.
- Richerson, Peter J., Robert Boyd & Robert L. Bettinger. 2009. Cultural innovations and demographic change. *Human Biology* 81, 211–235.
- Sampson, Gregory. 2002. Exploring the poverty of the stimulus. *The Linguistic Review* 19, 73–104.
- Savage-Rumbaugh, E. Sue & Roger Lewin. 1994. *Kanzi: The Ape at the Brink of the Human Mind*. New York: Wiley.
- Scott-Phillips, Thomas C. 2008. On the correct application of animal signalling theory to human communication. In Andrew D. M. Smith, Kenny Smith & Ramon Ferrer i Cancho (eds.), *The Evolution of Language: Proceedings of the 7Th International Conference (EVOLANG7)*, 275–282. Singapore: World Scientific.
- Smith, Kenny & Simon Kirby. 2008. Cultural evolution: Implications for the human language faculty and its evolution. *Philosophical Transactions of the Royal Society B* 363, 3591–3603.
- Sperber, Dan. 2000. Metarepresentations in an Evolutionary Perspective. In Dan Sperber (ed.), *Metarepresentations: A Multidisciplinary Perspective*, 117–137. Oxford: Oxford University Press.
- Sperber, Dan & Deirdre Wilson. 1995. *Relevance: Communication and Cognition*, 2nd edn. Malden, MA: Blackwell.
- Steels, Luc. 2009. Cognition and social dynamics play a major role in the formation of grammar. In Derek Bickerton & Eörs Szathmáry (eds.), *Biological Foundations and the Origin of Syntax*, 345–368. Cambridge, MA: MIT.
- Sterelny, Kim. 2003. *Thought in a Hostile World: The Evolution of Human Cognition*. Malden, MA: Blackwell Publishing.
- Steward, Julian H. 1955. *Theory of Culture Change: The Methodology of Multilinear Evolution*. Urbana, IL: University of Illinois Press.
- Stiner, Mary C. 2002. Carnivory, coevolution, and the geographic spread of the genus homo. *Journal of Archaeological Research* 10, 1–63.
- Thomason, Sarah Grey. 2001. *Language Contact*. Washington, DC: Georgetown University Press.
- Tomasello, Michael. 2008. *Origins of Human Communication*. Cambridge, MA: MIT Press.
- Tooby, John & Leda Cosmides. 1989. Evolutionary psychology and the generation of culture — 1. Theoretical considerations. *Ethology and Sociobiology* 10, 29–49.
- West, Stuart A., Ashleigh S. Griffin & Andy Gardner. 2007. Social semantics: How useful has group selection been? *Journal of Evolutionary Biology* 21, 374–385.
- Whiten, Andrew & Richard W. Byrne. 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge: Cambridge University Press.
- Wiessner, Polly. 2002. Hunting, healing, and hxaro exchange: A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human*

Behavior 23, 407–436.

Wiessner, Polly. 2005. Norm enforcement among the Ju/'hoansi Bushmen: A case for strong reciprocity? *Human Nature* 16, 115–145.

Yengoyan, Aram A. 1968. Demographic and ecological influences on aboriginal Australian marriage systems. In Richard B. Lee & Irven DeVore (eds.), *Man the Hunter*, 185–199. Chicago, IL: Aldine.

Peter J. Richerson
University of California, Davis
Department of Environmental Science & Policy
One Shields Avenue
Davis, CA 95616
USA
pjricherson@ucdavis.edu

Robert Boyd
University of California, Los Angeles
Department of Anthropology
375 Portola Place
Los Angeles, CA 90095
USA
rboyd@anthro.ucla.edu