

Evolving Honest Communication Systems:

Kin Selection and "Mother Tongues"

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(To appear in: *The Evolution of Communication Systems: A Comparative Approach* (Ed. by Oller, D. K. & Griebel, U.).

Cambridge, Massachusetts: MIT Press.

In a famous passage, J B S Haldane (1955) conveyed the seed of the idea of kin selection when he acknowledged the selective advantage of saving, at risk to his own life, drowning brothers or cousins, but not more distant relatives. In an odd turn for so insightful a biologist, he then concluded that it was highly unlikely for such logic to explain known examples of altruism. Haldane's reasoning was simple and logical: in a large population the average relatedness would be much smaller than the 1 in ten risk of drowning, and it would indeed be unprofitable, genetically speaking, to jump to the aid of a randomly-chosen individual. What is peculiar is that Haldane overlooked the fact that a "gift" of altruism, if bestowed selectively to closely-related kin, could easily be selected for, thus leaving it to Hamilton (1964) to comprehend and formalize inclusive-fitness theory, and make the most significant contribution to evolutionary theory since Darwin. Indeed, such "altruistic" acts need only satisfy Hamilton's famous equality $B_r > C$, (the Benefit to kin, as diluted by their fraction of relatedness r , must exceed the Cost to self), for selection to favor the action. Perhaps Haldane's reluctance to acknowledge this possibility was influenced by his own rather unusual experience of twice saving a drowning individual, when he gave no conscious thought to relatedness. The unsavory implications of doing otherwise were resurrected by the term "nepotism" associated with early experimental work on kin selection in the 1970's (e.g. Sherman, 1977). Perhaps distaste for nepotism partially accounts for the fact that kin selection has only slowly begun to be integrated into mainstream theory on the evolution of communication (Grafen, 1979; Maynard Smith, 1978; Maynard Smith, 1991; Maynard Smith, 1994; Johnstone & Grafen, 1992a; Godfray, 1991; Lachmann & Bergstrom, 1998; Bergstrom & Lachmann, 1998b)

My aim in this chapter is to help move this process of integration forward, particularly in the context of the evolution of human language, where the intersection between kin selection and communication theory appears to have considerable implications. I will refer to systems of communication that have evolved in a context of kin selection as "mother tongues", and will argue that such systems have very attractive theoretical properties for the evolution of rich communication systems like spoken language. Namely, mother tongues can be selected for accurate or "honest" communication (because senders and receivers sometimes have each others' best "genetic interests" at heart), and for semantic complexity (exchange of detailed information being thus valuable by increasing inclusive fitness, to a theoretical limit set only by the complexity of senders' and receivers' mental structures). I will suggest that these dual virtues allow mother tongues to evade the evolutionary traps of constant Machiavellian deceit, or wasteful Zahavian handicaps, that can bedevil communication systems among nonkin.

Furthermore, in some cases, selection on mother tongues will favor complexity for its own sake, allowing the formation of "kin dialects" which increase the accuracy of kin recognition. This observation, when applied to human language, may account for the otherwise very curious fact that language seems more complex than necessary for communication, in the sense that our ability to recognize regional, class or other dialects far exceeds the needs of semantic communication. Great English authors like Vladimir Nabokov or Joseph Conrad (born in Russia and Poland respectively), despite enormous grasp and fluid command of the English language, still spoke with an accent and sounded detectably "foreign" to native English speakers. Highly sophisticated concepts are exchanged between native and non-native speakers on a daily basis, throughout the world, but these speakers nonetheless perceive each others' speech as distinctly different. These everyday facts are inexplicable if human language evolved solely for purposes of semantic communication: why should our phonological system accurately reproduce a greater complexity than needed to efficiently transmit propositional information? I will suggest that this can be easily accounted for if the existence of such dialectal variation increases the ability of distant kin to recognize each other, and thus allows selective transmission of valuable information among kin.

In this paper I provide a brief introduction to some relevant evolutionary theory (including kin selection and theory on the evolution of communication) and consider some of the selective forces previously proposed to underlie the evolution of human language. Then I will advance the argument for mother tongues, reviewing known examples of kin-specific communication in nature and relating them to the evolution of extended parental and sibling care in birds and mammals. The massive transmission of information that occurs during the extended learning periods of childhood in many higher vertebrates can strongly select for vocal systems which aid this exchange even slightly. These are the conditions, I argue, that lead to many of the honest low-cost signals believed to represent mother tongues in animals, including squirrel alarm calls, primate grunts, the purrs of cats and other carnivores, ultrasonic calls of rats, signature whistles in dolphins, and others. Despite their ubiquity, such systems appear to lack the structural complexity that would be necessary to convey arbitrarily complex thought, as human language does. Paradoxically, the most structurally complex communication systems in nature, other than human language, are probably the learned passerine bird and humpback whale "songs", which as far as we know convey no propositional information at all. I propose that it was the co-occurrence of mother-tongue selection with additional forces selecting for structural complexity that provided the apparently unique evolutionary conditions within which language evolved, and suggest that one of these additional forces was the use of dialects to identify distant and previously unknown kin. Beyond a certain critical mass of communicators, the large shared pool of information made available to a widely-extended kin group becomes a highly-adaptive resource, and almost irresistibly selected for. The mother tongue hypothesis thus bypasses many of the problems currently plaguing neo-Darwinian theories of the evolution of language, as well as identifying numerous relevant points of contact between human language and communication systems in other animals.

Background: Kin Selection, Signaling Theory and the Evolution of Language

Altruism & Kin Selection: The notion of kin selection and the theory of inclusive fitness represent the most important contribution to evolutionary theory in the 20th century, and provides an explanation for "altruistic" phenomena, such as sociality in insects, that deeply troubled Darwin. The central notion, as already intuited by (Haldane, 1955), was that fitness is not simply a factor of an individual's survival, nor its success at producing offspring, but also the reproductive success of all those relatives who share its genes (Hamilton, 1964b; Hamilton, 1964a). To the extent that an individual's actions aid relative's survival or reproduction, at a minor cost to itself, they will increase its overall inclusive fitness. This (in retrospect rather intuitive) concept of inclusive fitness has important implications for the evolution of social behavior.

Hamilton realized that, from a gene's perspective, the critical question is not the survival of a particular mortal body in which it finds itself, but in the propagation of copies of itself in any body. Hamilton further realized that any mechanism whatsoever that allowed altruists to "donate" their resources selectively to kin would be powerfully selected for, as long as the exchange met the condition that

$$C < Br$$

where C is the cost to the donator, B is the benefit to the receiver and r is the fractional coefficient of relatedness (between 0 for unrelated individuals and 1 for clones or identical twins), which acts to "discount" the benefit accrued by the recipient. Any act for which the benefit to the recipient, discounted by its relatedness, exceeds the cost to the donator, shall increase the donator's inclusive fitness, and should be selected for. This reasoning provided an immediate solution to the problem of the "altruism" of female honeybees, ants and other eusocial insects, who cooperate to raise their sisters, and protect them at the cost of their own lives, while bearing no young themselves. This problem was a serious worry for Darwin, who saw honeybee altruistic behavior as directly contrary to his theory of natural selection. In the framework of inclusive fitness, eusociality follows directly from a genetic peculiarity of Hymenopteran insects, which results in sisters being more closely related to one another than they are to their own offspring (Wilson, 1975).

A second theoretical explanation for apparently altruistic acts does not require kinship. This is known as "reciprocal altruism" (Trivers, 1971), in which two unrelated individuals mutually benefit by taking turns exchanging resources at times when the cost to the donor is low and the benefit to the receiver is high. Such behavior requires a rather special set of circumstances, and empirical demonstrations of reciprocal altruism in nature are rare at best. (Note that the claim of (Packer, 1977) of reciprocal altruism in baboons has repeatedly failed to replicate (Bercovitch, 1988), and the exchange of blood by vampire bats studied by (Wilkinson, 1984) was almost entirely among kin). Thus despite the ubiquity of reciprocity in human society (the entire global economy can be thought of as a huge, institutionally-regulated system of reciprocal altruism), the available evidence suggests that such systems are very

rare in animals, in sharp contrast to kin-selected systems which are very common. Despite the obvious fact that modern human languages are used by non-kin to reciprocally share information, contemporary language is always used quite intensively among kin and there is no *a priori* reason to assume a preponderance of non-kin communication in early stages of language evolution. Kin communication, with ubiquitous nonhuman examples known, may provide an easy evolutionary route to reciprocal sharing among non-kin, but the converse is not true. Thus, in what follows, I will focus on kin selection and make little mention of reciprocity among non-kin.

Honest Signaling Theory: "Honest" signals are those which accurately (though not necessarily perfectly) convey some information about some relevant quality of the signaler (e.g. its species, sex, size, condition, etc.) (Dawkins & Guilford, 1991). Like many terms in modern ethology, this one should be interpreted in the technical sense just given, not by the layperson's model of human honesty, which includes assumptions of self-knowledge, intention to communicate and various other complications. Thus, if a newborn baby cries only when requiring care, this is an "honest" signal, despite the fact that few would attribute honesty, in the ordinary sense, to newborns. Below I will dispense with the quotation marks around the term, with the understanding that "honest" is being used in its technical sense throughout.

A long tradition in ethology assumed that much communication evolved to facilitate honest communication, particularly among kin (Dawkins & Krebs, 1978; Hinde, 1981). This assumption came under strong attack in several seminal papers by Amotz Zahavi (Zahavi, 1975; Zahavi, 1977), which spurred a large and still growing literature on the theory of honest signaling. The central claim of Zahavi's attack, echoed less forcefully in (Dawkins & Krebs, 1978), is that such honesty cannot be simply assumed. In fact, natural selection should in many cases favor animals which are deceitful (again in a non-cognitive sense) if dishonest behavior leads to personal advantage and increased reproductive success. This is easily understood when we consider the advantages obtained by liars and cheats in human society if they escape detection and punishment. By highlighting the readiness with which Machiavellian deceit can destabilize honest signaling systems, this perspective essentially turned the tables, suggesting that the real question for theorists interested in the evolution of communication is why any signaling systems are honest (if indeed they are). Zahavi's proposed solution to this question, the "handicap principle," embodies a rather non-intuitive claim: that honest signals are possible only when the signaler pays a high cost when emitting the signal. According to Zahavi (Zahavi, 1993), such costs are necessary if a signal is to stay honest and remain in circulation over evolutionary time. Despite early critiques of this idea from a mathematical viewpoint (e.g. (Maynard Smith, 1976)), the handicap principle received theoretical support from a complex mathematical model of signaling introduced by Grafen (Grafen, 1990a; Grafen, 1990b) and has since generated a weighty volume of theoretical work, along with a less impressive body of empirical work. Recently some results of early theoretical work were discovered to be dependent on errors in the original papers (Siller, 1998). It is far beyond the scope of this paper to review all of this literature, much of

which is highly technical, (see Johnstone, this volume, for a more detailed introduction). Thus I confine myself here to three major themes that have emerged from this literature.

Any signal obviously bears some cost (even if only the time wasted not doing something else)(Maynard Smith & Harper, 1995). Unless the handicap principle requires more stringent conditions on signaling costs than their simple existence, it reduces to this obvious and uninformative fact. Empirical demonstrations of a cost of signal production thus provide no support for the handicap principle, which demands additional "strategic" costs over and above those necessary to produce a detectable signal. When the costs of signals have been measured, highly costly signals appear to be the exception rather than the rule, contrary to the predictions of the handicap principle. For example, vocal signals in many vertebrates appear to have surprisingly low metabolic costs (Chappell et al., 1995; Horn et al., 1995; McCarty, 1996), while still maintaining honesty; the same is true of human speech. Various signals, such as piloerection ("raising the hackles") or crest erection in birds, appear to have virtually no physiological costs but are extremely common, (Marler, 1968; Wilson, 1972). Furthermore, signaling systems evolve within a context of physical and physiological constraints which may make honesty difficult or impossible to escape (Maynard Smith & Harper, 1995). In such cases honesty is the default condition and it is dishonesty which demands an adaptive explanation ((Fitch & Hauser, in press)). An example are formant cues to body size which are present in vocalizations of many birds and mammals. Formants are the resonances of the vocal tract, and their frequencies depend on the length of this tube of air in a manner that follows from basic acoustic laws. Because (in most cases) vocal tract length is itself necessarily correlated with body size, formants provide a "free" cue to body size in any vertebrate that produces a vocalization (Fitch, 1997; Fitch & Giedd, 1999). Such size information does not cost anything extra to encode: it is present as a result of the physics of sound production and the anatomy of the vocal production apparatus. Although selection has acted in some cases to exaggerate these formant cues by elongating the vocal tract beyond its normal anatomical confines (Fitch & Reby, 2001; Fitch, 1999), it is this deception which is an adaptation, not the original honest signal which existed, and was stable, by default.

Second, an important limitation of much of the early signaling theory is that it did not include the costs and benefits to receivers, implicitly assuming the "assessment costs" to be at or near zero. Later work redressed this oversight, both by focusing on the costs to receivers of eliciting or evaluating signals (Dawkins & Guilford, 1991), or on the effects of less-than-perfect signal reception (Wiley, 1994; Johnstone & Grafen, 1992b). These results again weaken the central claim of the handicap theory, showing that "conventional" signaling systems, which convey some information most of the time, but tolerate a low level of deceptive signaling, can be more stable evolutionarily than totally honest systems which exact a high price from both signalers and receivers. A nice example of the cost of assessment are red deer roaring battles, in which rival males must engage in a potentially exhausting (and dangerous) roaring display in order to incite a resident male to roar at full strength (Clutton-Brock & Albon, 1979). The costs paid by receivers are clearly non-negligible in this well-studied case (though it appears that various physical constraints may provide an additional guarantee of some level of

honesty (Fitch & Reby, 2001)). In general threat displays should tolerate some level of bluffing, because the costs to intruders of "probing" could be severe bodily injury if the signaler is NOT bluffing (Adams & Caldwell, 1990). Similarly, it may not pay a female choosing a mate to spend weeks evaluating the quality of her potential mates. Instead the best strategy can be to choose one who looks or acts like a past good mate, or even simply choose the male that other females are mating with (e.g. (Losey et al., 1986)). These issues are important, and virtually ensure that evolution will not fill the world with arbitrarily costly signaling systems. However, while such considerations are important in understanding the limits of the handicap notion, they are less relevant in the quest for cheap, honest signaling systems that I am concerned with here. Their main importance in the context of the evolution of language is that the cost of discovering the truth provides a theoretical model for how a low level of dishonesty can persist indefinitely in a basically honest system. Such a characterization would appear to fit human language rather well, and perhaps can account for the obvious fact that, despite its undeniable (and quite remarkable) capacity for honest transmission of information, language is not always used honestly.

Finally, the most significant modification of honest signaling theory comes from a consideration of communication among kin. This issue has been studied in the context of the Sir Philip Sydney game, introduced by (Maynard Smith, 1991), a stylized theoretical framework in which an individual must decide whether to donate some indivisible resource to a needy relative. Donation to a relative in this framework allows a potential inclusive fitness benefit to the donor at an immediate cost to the donor. Maynard Smith found that an honest signaling system can evolve in the presence of low or zero, cost to the signaler if sender and receiver interests do not conflict (technically, if the outcomes are ranked equivalently by both participants). Further models have extended this theory (e.g. (Godfray, 1991; Johnstone & Grafen, 1992a), also suggesting the possibility of low signaling costs for closely-related individuals. This work, especially that concerning begging by offspring from their parents, has been tested empirically as well, and very low physiological costs have been measured in beggin nestling birds (McCarty, 1996). More recently, an important series of papers have found that when certain assumptions of earlier models are relaxed, multiple low-cost, or cost-free stable signaling systems can evolve among kin (Bergstrom & Lachmann, 1998b; Bergstrom & Lachmann, 1998a; Lachmann & Bergstrom, 1998). Thus given the partially shared genetic interests among kin, cheap or free honest communication systems can evolve and will be evolutionarily stable.

Animal Mother Tongues: Kin communication in other species

I'll now give a brief and selective overview of kin communication in animals to highlight some of the empirical work that has been done on this topic. There are a number of interesting phenomena that could be mentioned but I'll stick to three: food calls as an aid to food learning, nestling begging calls, and alarm calls. I'll focus on the latter, which has the largest body of empirical work devoted to it.

In contrast to altricial birds which are typically born totally blind and helpless, and are fed by the parents for days or weeks after birth, many precocial birds such as grouse, ducks and chickens must

essentially feed themselves from a very early age. In such species, it is quite common for the young to follow their mother, providing an opportunity to learn by example from her behavior. The existence of food calls, emitted when sighting food or feeding on it, provides a nice example of a very simple form of kin communication that can transmit useful, learned information about what is (or is not) edible. Simply by feeding on a particular substance, and emitting food calls to attract the attention of her young, a mother provides an opportunity for her children to benefit from her past experience and thus bypass a certain amount of trial and error learning. This may be the simplest example of kin communication that helps transmit learned information, and to be valuable it requires no explicit "teaching" or sophisticated mental model of offspring knowledge. A similar example is provided by migrating birds. In many species juveniles accompany their parents on the first long-distance migration and thus learn safe migration routes and stopping points (Matthews, 1968).

Many birds and mammals emit characteristic calls at the appearance of predators, which alert conspecifics to the predator and often immediately elicit escape reactions. The existence of such "alarm calls" in birds and mammals was recognized as a problem by evolutionary theorists four decades ago (Hamilton, 1964b; Maynard Smith, 1965), and played an important role in the development of kin selection theory. The problem is simple: from an individually selfish viewpoint, why should an organism spotting a predator vocalize, and thus call attention to itself, when it could just slink away, leaving its unsuspecting groupmates to be attacked? Although various "selfish" proposals have been offered, e.g. that the call deters predators from repeated hunting at that site (Trivers, 1971; Sherman, 1985), these are seen as relatively implausible compared to the alternative: that calls serve to warn kin and thus increase inclusive fitness. The mathematical prerequisites for this are quite simple (Hamilton, 1964b; Maynard Smith, 1965; Charnov & Krebs, 1975): the alarm call must be relatively low-cost and the species must inhabit groups that contain kin. During the 1970's, a wealth of comparative data were gathered on this topic, mostly from ground-living squirrels, that provide strong empirical support for this kin-communication hypothesis. In two seminal papers (Dunford, 1977; Sherman, 1977), different species of ground squirrel, females with kin present were found to be the predominant alarm callers (males were silent, except as juveniles living with their mothers and siblings). Males in general, and newcomer or transient females, did little alarm calling. Sherman's paper further demonstrated a cost to calling: callers were significantly more likely to be killed than non-callers. Further data on other species substantiated these conclusions (Hoogland, 1983; Smith, 1978; Barash, 1976) with the interesting twist that, in those species where males participate in parental care and/or live amongst kin, males also call. Although it may be the case that much of the alarm calling serves to protect an individual's offspring, Sherman (Sherman, 1980) provides data indicating that offspring are not the only kin "protected" via alarm calls, and therefore that alarm calls are kin-communication in the wider sense, not just parental care (Shields, 1980).

Of course, once a proclivity for alarm calling in general is established, kin selection might also act to increase the specificity of the calls, for example to distinguish aerial from ground predators, an elaboration observed in a wide variety of bird and mammal species (Klump & Shalter, 1984), including

nonhuman primates (Seyfarth et al., 1980). The "honesty" of these differentiated signals is easy to explain in the context of kin selection: to the extent that there are different optimal escape strategies for different classes of predator, an individual will increase its inclusive fitness by emitting calls different enough to allow listening kin to adopt the best escape strategy. Note that this does not require intent to label different predators on the part of the caller: a simple difference in arousal caused by different predators would suffice, if it leads to discriminable differences in call acoustics (Owings & Hennessy, 1984; Seyfarth & Cheney, 1997). Screams of surprise might reliably signal less dangerous predators than screams of terror. Thus one does not have to posit intentional "predator labeling" to understand the adaptive value of signal elaboration in the context of kin-selected alarm calls. Of course, the number of differentiated signals that are necessary in this context will be limited by the number of predators (or more generally, of types of danger that require differing responses). Even in the case of highly preyed-upon species like vervet monkeys (with 16 known predators, (Cheney & Seyfarth, 1981)) or Belding's ground squirrels (with 9 known predators, (Sherman, 1985; Sherman, 1977)), alarm calling alone will never lead to an infinitely extensible set of vocalizations. Thus, alarm calls provide strong selection for honest communication, but not for unbounded generativity.

Lest it be thought that ALL kin communication is harmonious, the work on nestling begging must be mentioned. Nestling begging is a type of kin communication that has been studied from both theoretical (e.g. (Godfray, 1991)) and empirical perspectives ((McCarty, 1996; Briskie et al., 1994; Haskell, 1994)). Begging involves food as a benefit (not just information), and so differs considerably from the above two examples of mother tongues. The competition between nestmates for food can be extremely fierce in birds, sometimes leading to siblicide, and thus it would be unsurprising if some "dishonest" begging occurred. However, the evidence from metabolic rate suggests that begging is not particularly costly ((McCarty, 1996)), and no clear examples of dishonesty are known, even in this highly competitive situation. The use of acoustic signals to acquire food or other resources from the parents may lead to a much greater degree of sibling competition and/or parent/offspring conflict than if the young are being "fed" information, at low physiological cost, by the parents.

To summarize, I have argued that mother tongues provide, in many cases, the preconditions for the evolution of honest, low-cost (or "cost-free") communication systems. Using the prototypical example of alarm calls, I showed that such systems are probably common, if not ubiquitous, in kin-group-living mammals. Thus the theory of mother tongues, by focusing on the genetic common interests of kin, seems to satisfy one of the primary desiderata for a theory of language evolution: honest communication without handicaps. I submit that this is an important point in its own right. I also admit that it seems (to me at least) relatively obvious; hence my surprise that this hypothesis appears to have escaped explicit mention by previous theorists, who have typically focused on communication among non-kin adults when discussing language evolution.

Critical Hurdles in the Evolution of Language

The brief overview of signaling theory above shows that, from the viewpoint of natural selection, honesty is not always the best policy, and that when honesty exists, it demands an explanation. This has some important implications for the evolution of human language. Spoken language is low-cost (see below) but has an unparalleled capacity to honestly convey detailed and arbitrarily complex information. Thus language is quite anomalous from the viewpoint of handicap theory (Zahavi, 1993), which has led many recent writers to highlight this apparent discrepancy (e.g., (Zahavi, 1993; Dessalles, 1998; Knight, 1998; Power, 1998). Of course the discrepancy is only troubling to the extent that the handicap principle itself is true. The main point of the review above is that communication systems evolving among kin do not have to obey the strictures of handicap theory (whether other systems do is a separate question). While it is true, as mentioned above, that cheap honesty can evolve as a result of other constraints, it seems highly unlikely that receiver error or physical constraints (e.g. on the acoustic cues to body size) could account for the capacity of language to be both highly accurate and open-ended. Humans are not restricted to discussions of relative body size. Thus it seems worth considering the thesis of this paper: that human language evolved in a context of communication among kin.

As many commentators on the problem of language evolution have remarked, language is so different from the communication systems of other animals that the very comparison may seem strained. However, it is equally clear that there are fundamental biological similarities between humans and animals, both in terms of neural functions (there are no new neurotransmitters, or new types of neuron in humans) and genetics (virtually all of our genes are shared with mice, and the sequence similarity of these genes is probably around 98% between chimps and humans). Further, many aspects of human language are built on a foundation shared with other animals (these include, uncontroversially, most aspects of the vocal production and hearing apparatus, the system of long-term memory that must underlie the lexicon, and rather complex conceptual structures including memory of places, events and individuals). An important issue to be faced by any theory of language evolution is thus how to conceptualize the undeniable differences between language and other communication systems in a manner that neither trivializes the differences nor neglects the similarities, both of which are important. To my mind, a natural framework within which to understand language evolution is comparative, that is, in comparison to the many animal communication systems that are now reasonably well-understood. A comparison of language and animal communication systems allows us to identify important differences along with key similarities, both homologies (probably present in our prelinguistic ancestors) and analogies (repeatedly evolved solutions to some common problem) (Hauser, 1996). This approach highlights difficult evolutionary problems that were solved, somehow, *en route* to modern language. These are, in no particular order:

1. Cheap Honesty: an ability and propensity to communicate rich and accurate information, at low cost;
2. Vocal Imitation: an ability to learn and reproduce arbitrary acoustic signals; and
3. Complexity (Discrete infinity): an ability to generate an open-ended system of words & sentences.

While the combination of these capabilities appears unique to humans, each of these three basic capacities has at least some parallels in the animal kingdom. While there are many examples of either information-poor systems (e.g. most bird songs appear to have little meaning beyond "I'm a male of species X, other males stay away, females approach") or actively deceitful systems (some bird alarm calls are used deceptively as frequently as 60% (Møller, 1990; Møller, 1988; Munn, 1986)), there are also "honest" systems in nature that convey accurate information (e.g. mammal alarm calls) including information about events that are not perceptually present (e.g. honeybee dance). Vocal imitation is also well-developed in other species, though not apparently in other primates [Janik, 1997 #2591; Fitch, 2000 #2659 - most birds have a capacity for vocal learning and some, such as mockingbirds, have a rich capacity to imitate not only bird calls but also many environmental sounds.

Finally the ability to generate an open-ended and potentially infinite variety of words (phonology) and sentences (syntax) by recombining smaller units, seen in all human languages, has often seemed qualitatively different from the capacities of any other animal. At two different levels, modern human languages can generate infinitely diverse and complex structures: at the level of phonology (which generates new words from meaningless phonemes) and of syntax (generating new phrases or sentences). This abstract property follows from the manner in which language generate their structures by recombination of a finite set of primitives (phonemes/syllables in phonology, or words in syntax). Any word can be extended by adding various affixes (as in adding "non-" to "disestablishmentarianism") and any sentence by adding new phrases (as in adding "John believes that" to "Mary will exceed the expectations of the committee"). Although these generative systems have important differences (e.g., most syntactic generation is done on line, producing novel utterances, while the products of phonological and morphological generation are typically memorized in a stored lexicon), the critical factor in both systems is flexible, open-ended generation of novelty by recombination of discrete elements (Studdert-Kennedy, 1998; Nowak et al., 1999).

This concept of discrete infinity has occasionally been criticized because, in reality, we produce neither infinitely long words nor infinitely long sentences. These limitations appear to be a matter of implementation limitations (of memory, time, breath or whatever) rather than some intrinsic limitation of the principles of phonology or syntax *per se*. I agree that such limitations play an important role in the neural implementation and evolution of language, and do not advocate ignoring them. However, I don't believe that these facts justify neglecting the basic productivity of language which is so central to its functioning, and so different from most other communication systems. To avoid needless argument, I will refer to language as being "highly generative" rather than "infinitely generative", because the key consideration is the vast difference between human language and other communication systems, rather than infinity *per se*. The songs of birds or whales use recombination of basic units to form larger, more complex units, and there are no obvious limits on the variety of the units thus formed. Although these larger units appear to be ends in themselves, rather than a vehicle for transmitting detailed messages, they are richly generative nonetheless (a similar point could be made

about melody in music: there is no known limit to the number of possible melodies, although these variant structures convey no obvious propositional meanings).

Summarizing, the combination of honesty, vocal imitation and generativity appears to be unique to *Homo sapiens*, despite the fact that analogs to each capability are observed in other species. That these abilities are necessary for language should be relatively uncontroversial; whether they are sufficient is certainly not. For instance it is widely recognized that modern language relies heavily on a detailed notion of the contents of other minds, often termed a "theory of mind", and that pragmatically well-formed communication would be impossible without this. However, this ability may exist in apes, and thus was probably present in our prelinguistic ancestors ((Povinelli et al., 1990)), so it seems that theorists of language evolution can take it for granted. More controversially, many workers suggest that a much more complex set of abilities, including detailed innate constraints on both phonology and syntax summed up by the phrase "universal grammar", are also necessary ((Pinker & Bloom, 1990; Jackendoff, 1999). I will make no commitment on this issue here. There is enough controversy among modern linguists about the structure of UG, and enough flux and change in whatever consensus exists, as to limit the suitability of this concept as a target of inquiry for evolutionary biologists. My present goal is to explore the evolution of cheap honesty, discrete infinity and imitation, rather than debate the details of UG and its evolution (see, e.g. (Jackendoff, 1999; Bickerton, 1995; Nowak et al., 2001)). All workers should agree on the necessity of the above three components in one form or another, though they might prefer different formulations or terminology to pick them out.

Previous Theories for the Selective Value of Language

Any evolved capacity can be explained in terms of mechanisms (anatomy, neural circuitry, etc.), ontogeny (the developmental pathways that construct the capacity), phylogeny (the history of the evolution of the trait) and function (the fulfillment of which provided the selective advantage of the capacity). These explanations are complementary, rather than providing contrasting alternatives (Tinbergen, 1963). While a complete understanding of a trait would necessitate answers to all of these questions, they are conceptually separate and can be treated alone. In this paper I will discuss only the functional side of the components underlying language. My goal is to explain the adaptive function of the key components of imitation, complexity and honesty, making as few *a priori* assumptions as possible. I do not assume that the function for the three components was the same, nor that they evolved simultaneously, nor that their function today in modern language is necessarily the same as their original function. I will not discuss the evolution of the mechanisms of speech production or perception (for this see (Lieberman, 1984; Lieberman, 2000; MacNeilage, 1998; Liberman & Mattingly, 1985)) nor the phylogenetic history of language (in australopithecines, *Homo erectus* or Neanderthals). The question posed here is what selective advantage language ability gave to its first users, whoever they were.

Some have questioned the very notion that language is adaptive, suggesting that language is a "spandrel" - a nonadaptive by-product of some other trait such as large brains. This viewpoint may

derive from a misinterpretation of a technical use of the term "language" to pick out certain core aspects of syntax. Clearly, certain aspects of language will be nonadaptive byproducts of other changes (as for virtually any trait), and it is possible that some aspects of syntax may be among these. However, this cannot be the case for language as a whole: the complex set of interacting subsystems that constitutes the language capacity in the broader sense, which includes the perception and production of speech (phonetics, phonology), the manipulation of hierarchically structured phrases and sentences (syntax) and their interpretation both literally (semantics) and in current context (pragmatics). This complex could not result from genetic drift, physical constraints, or correlated change, but has all the earmarks of an adaptation (Lieberman, 1984; Pinker & Bloom, 1990). It is this whole that I aim to understand in a selective context.

It has also been questioned whether the most important function of language, particular in its syntactic particulars, is communication. While the powerful generativity and structure provided by language probably has value beyond communication (e.g. solely for more elaborate or articulated thought), such non-communicative generativity is not by itself adequate to explain the generativity of human language. Humans clearly are able to use their generative capabilities in communication, and the phonological system which allows this seems extraneous from the viewpoint of "pure thought". Furthermore, even when modern humans use language to think privately, we "hear" the sounds of words in our heads (and can compute rhymes, count syllables, etc), meaning that even private language makes use of this external, socially-shareable component of language. Thus, it is important to consider the possible evolutionary grounds for such capabilities in the context of communication, and of animal communication systems.

Not all writers on language evolution have been clear about exactly which aspects of language they intend to explain, nor on what level (functional, mechanistic, etc.) they are attacking the problem. Often discussions of adaptive function and mechanism are mixed indiscriminantly (e.g. (Bickerton, 1998)). Nonetheless, there are abundant hypotheses as to the selective value of at least some aspects of language, which I will now briefly, and selectively, review.

Most previous authors have focussed on the role of linguistic communication among adults, with very little comment on its role in transferring information between parents and offspring. In particular, a conviction that complex language serves to increase an individual's reproductive success directly, by making the speaker attractive to potential mates and thus increasing fecundity, appears to be taken for granted by an otherwise diverse group of authors (e.g. Bickerton, 1998; Miller, 2001; Pinker & Bloom, 1990; Lightfoot, 1991). For example, "females would surely have preferred mates whose communicative capacities so strikingly outclassed those of other available partners" (Bickerton, 1998 #3586, p 353), and "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, 1990 #1092, p. 725). Note that there is no good data indicating a link between linguistic complexity and mating success in humans (despite the apparent appeal of a putative link between complex oration and

mating success in academic circles). Thus it seems peculiar that so many scholars assume that "better grammar led to more sex" in our evolutionary history. The exceptions are surprisingly few.

Several recent authors have suggested that the wider social role of language played a key role in its evolution, focusing on the mounting evidence for the role of social intelligence in the evolution of nonhuman primates. Traditionally it has been assumed that the large brains of nonhuman primates, and probably humans as well, result from selection for increased behavioral flexibility, spatial memory and other factors aiding survival ecological generalists. The "Machiavellian intelligence" hypothesis (Byrne & Whiten, 1988) suggests in contrast that it is the increased social complexity of group living primates that has fueled the dramatic increase in neural horsepower that characterizes evolution in the primate order. These authors point out that large stable groups pose serious information processing problems - just remembering identities and past interactions with twenty or more group members might be challenging for the average mammal, and primates deal in a social world where the interactions and relationships among all those individuals are also important. Robin Dunbar has suggested (Dunbar, 1993; Dunbar, 1996) that these social pressures increased to the breaking point in early hominids, when group size (he suggests) grew above a limit imposed by grooming time in other primates. Dunbar's "gossip as grooming" hypothesis extends the Machiavellian intelligence notion, suggesting that language arose primarily as a solution to the problem of group cohesion created under these circumstances. By this hypothesis, language exists primarily to exchange information about other group members, and thus to establish and cement social relations within small coalitions or subgroups. A similar idea is proposed by (Bickerton, 1998), who suggests that the neural mechanisms initially evolved for social intelligence (particularly "theta analysis" - who did what to whom) were exapted into the new realm of processing syntactic structure. In contrast to Dunbar, Bickerton suggests that this exaptation functioned to increase mating success, rather than success at maintaining social cohesion or coalitions.

Terrance Deacon (Deacon, 1997) has proposed that the selective value of language arose from its value in stabilizing the relationship between monogamous males and females, a relationship that became necessary as human children became an increasing burden, demanding more care than a single individual female could provide. By this hypothesis, the intrinsic instability of parental monogamy (which is extremely rare in mammals) required some stabilizing mechanism, and language arose to fill this need. Both the ability to have rational discussions of past and future between the mates themselves, and the ability for other group members to act as gossips who report extra-pair dalliances, are suggested to have been important in the evolution of our unusual linguistic ability to discuss the past and future.

Finally, as already mentioned, the proposed role of language in obtaining matings seems to be the most popular selective advantage ascribed to the linguistic proficiencies of our early hominid ancestors. First advanced by (Darwin, 1871), the idea that sexual selection played a key role in language evolution is appealing in its simplicity: in the contest for mates, there is a constant "arms race" among

different displays. For example, a choosy female observing males at a lek (leks are assemblages of displaying males which are visited by females in search of mates, found in many species of fish, birds, and mammals) might always choose the most complex display, perhaps because it originally provided some indication of the males quality (intellect, vigor, etc.). In such a situation, a male who could always "trump" a neighbor's display by repeating it with an additional element would clearly achieve high reproductive success. This basic and well-known idea (Fisher, 1930), has been recently rediscovered with much fanfare by evolutionary psychologists (e.g. (Miller, 2001)). Sexual selection thus provides the best explanation for the evolution of complex displays in many contexts, especially bird song and the songs of humpback whales. Note that the sexual selection hypothesis, in the context of language, only provides an explanation of imitation and complexity, providing no rationale for cheap honesty. Indeed, given the often opposing interests of male and female in the context of mate choice, it is rather difficult to see how honesty could persist in such a system at all. We can of course posit a two-stage model in which complexity for its own sake was selected first (e.g. as "song" in the mate choice context, (Darwin, 1871)) and then honesty was added in a later stage of evolution (e.g. in the mother tongue context, as suggested here). Such a model seems plausible, and consistent with a fair amount of the evidence concerning human evolution.

However, there are two critical problems with the sexual selection model for the evolution of language. First, sexually-selected traits are typically dimorphic, with the displaying sex expressing the traits either exclusively, or to a much greater degree than, the "choosing" sex. In most vertebrates, the displaying sex is male (the rare exceptions are in polyandrous birds like jacanas and painted snipe), and the choosy sex female. This is the situation virtually universally in mammals, and in primates: males are larger, more competitive in mating contexts, and display secondary sexual display characteristics to a greater degree than do females. If the complexity of language originated in sexually-selected displays, we would thus expect human males to have more complex and highly-developed linguistic capacities than females. In fact, just the opposite is the case: all available data suggests female linguistic abilities significantly exceed those of males to the extent that they differ at all (see Henton, 1992 for a review). Language abilities develops sooner in girls than in boys, women have larger vocabularies than men, and exceed men at tongue-twisters and other tests of speech abilities. Speech abnormalities such as stuttering, dyslexia or autism afflict males much more commonly than females.

Second, and more glaringly, most sexual display characters in the animal kingdom arise at puberty, concomitant with their initial utility in sexual maturity and the onset of mating. This is obviously not the case with human language which is remarkable in its precocity. Human linguistic skills are already impressive at 1.5 years, and in fact begin a steady decline at puberty, quite the opposite of what sexual selection would predict, or what we see in birds or whales. These discrepancies between the predictions of sexual selection theory and the facts of human language suggest the need for an alternative hypothesis for the selective value of human language. Even if generative complexity was "jump started" by sexual selection, it seems unlikely in the extreme that it achieved its present early-

onset, female-biased status due to sexual selection alone. These aspects of language are much more understandable if a key selective advantage of language was (and is) the transfer of information between kin, particularly parents and their offspring.

"Mother Tongues": kin-selected communication systems

Language differs from other primate communication systems in terms both of its reliance on detailed vocal imitation (a capacity not known in any other primate), and its open-ended generative complexity (a feature which may be unique, but has its nearest analogs in the non-propositional "song" of whales and birds). Perhaps most importantly, its capacity to honestly communicate arbitrarily complex information seems to be unique among known life forms (it may have its closest parallel in such communication systems as honeybee dance language). I suggest that the conditions for the evolution of these unusual characteristics are best met by positing that human language evolved as a "mother tongue" - a communication system used among kin, especially but not exclusively between parents and their offspring. Because the physiological costs of communicating via speech are low, the benefits of the information shared need not be particularly high for such a system to satisfy Hamilton's inequality and increase inclusive fitness. In turn, the use of a system to communicate among kin can avoid both runaway Machiavellian deceit, and wasteful Zahavian handicaps. In animals with very long childhoods, like humans, there is a potential value to the entire store of information that parents or siblings have accumulated, which means that there is pressure for increased complexity to transmit more detailed information. Finally, the characteristics of language are such that speech provides not just the intended information, but also dialectal information about the provenance of the speaker. I will suggest that one function of such extra-propositional information is to provide a cue for kin recognition, which enables even distant kin that have not met to recognize one another and share information preferentially. By enlarging the store of knowledge available in the kin group, this provides positive feedback by increasing the benefit of the other two aspects of the system. Thus, mother tongues could provide ideal circumstances for the three capabilities described above as central to human language. In the rest of this paper I will flesh out these notions, beginning with a more detailed consideration of costs and benefits.

From the viewpoint of kin selection theory, the evolution of honest communication between kin requires the satisfaction of Hamilton's inequality, $C < Br$. The costs to the signaler must be less than the benefits to the receiver, discounted by its coefficient of relatedness. If I am to yell "predator!" to my kin when I spot a predator, the benefit to my relatives (discounted by r) must exceed the cost to me, both the physiological cost of yelling (which is negligible), and the increased risk of myself being eaten that yelling might incur (which may not be).

The costs and benefits in Hamilton's equation are in terms of lifetime reproductive success (RS) or fitness, from a gene's viewpoint. As (Grafen, 1982) pointed out, the individual's inclusive fitness is NOT simply the sum of its own fitness, plus that of all its relatives discounted by r . This would incorrectly include that portion of the individual's RS that is due to help from others, as well as that

portion of theirs that is not due to its aid. (Grafen, 1982) has argued that the simplest measure of inclusive fitness is actually just individual RS, because that includes the increment of RS gained by help from its kin. Of course, in reality scientists rarely have access to such costs and benefits in terms of lifetime RS, and so various measurable proxies for fitness are adopted instead. Here I will attempt a breakdown of these short-term costs and benefits, which turns out to be surprisingly difficult.

Let us first consider benefits. As a first pass, one might try to measure the benefits in terms of information theory (Shannon & Weaver, 1949) which defines information objectively as reduction in uncertainty. Benefit might be seen as the number of bits necessary to encode the broadcast message. The simplest version of this is obviously wrong, because (to use a human example) the benefit to a receiver of a broadcast of the entire yellow pages may be less beneficial, in terms of fitness, than the few bits encoding my credit card number. Similarly, an alarm call is of no benefit to kin who have already spotted the predator themselves and undertaken evasive action. What matters is the amount of "relevant" information - the reduction of uncertainty about questions *the receiver needs an answer to*. Thus we would like a theory that can provide a measure of *relevant* information, in bits. To measure this requires an understanding (at least on the observing scientists' part) of what the receiver already knows, and might find relevant given the circumstances. Although an extension of information theory into the domain of relevance in language should be possible (and is a desideratum of relevance theory, and pragmatics in general, see e.g. (Sperber & Wilson, 1986; Dessalles, 1998)), such understanding will surely remain elusive in animals in the near future.

There are at least two ways of capturing the benefit of shared information. The first is not context dependent, and is simply the information exchanged via signaling that was not previously shared. This model is appropriate for parent-offspring exchange of information, where we can assume parents know many things that their offspring do not, and that any and all of this information is beneficial to the recipient. In this formulation, the "filtering" of relevant information is done privately, by the parent, prior to communication. By this simple model, anything important enough to be learned and remembered by the parent is potentially beneficial to its offspring. Although it is easy to think of exceptions to this notion, particularly in the rapidly-changing world of human technology where my understanding of carburetors or 8-track tape recorders is useless to my offspring, its primary strength is its simplicity and relative tractability.

A more complex measure of the benefit of information would take the current context into account. Unfortunately, defining "context" adequately causes major problems, and is perhaps impossible within the Shannon framework (Sperber & Wilson, 1986). Intuitively, information about which berries are edible is perfectly informative by the simple formulation above, but completely irrelevant if a predator is swooping down upon your unwitting offspring. A signaler that can select among the huge number of possible messages to transmit those few that are of immediate value is being "relevant" in the everyday sense. However, outside such simple examples of attacking predators, the notion of "context" becomes challenging to define, since anything could be relevant in principle, and so there is no

easy way to automatically exclude ANY information from the potential "context" (Sperber & Wilson, 1986). This apparently minor fact has quite serious implications, and has caused bad headaches for generations of computer scientists and philosophers, to whom it is known as the "frame problem" (Pylyshyn, 1987). At present, no adequate solution is available. Thus it will suffice here, I think, to use the simpler non-contextual formulation described above, which at least allow a discussion of the problem and is appropriate for parent birds helping their children learn what to eat, or early hominids conversing safely around a fire and exchanging information. Thus for the current discussion, benefits are in terms of the bits of information acquired by the recipient of a signal, relative to the cost of acquiring the same information by unaided trial-and-error learning. It should be noted that this is quite difference from the benefits in some other communication systems, which are often in terms of non-informational resources like food (in the case of begging calls) or mating (in the case of advertisement.)

We now turn to the costs of signaling. In the traditional Zahavian framework, the costs associated with signals were conceptualized as physiological costs. For example, oxygen consumption during vocalization in frogs and insects reveals very high metabolic costs relative to resting metabolism (Ryan, 1988), a result that has led some writers to conclude that all acoustic communication is very expensive (e.g. (Alcock, 1989)). This conclusion is erroneous. First note that "energetic cost" is typically defined relative to resting metabolism, or basal metabolism, so that costs are artificially inflated in cold-blooded organisms such as frogs which have a low resting metabolism relative to birds or mammals (Chappell et al., 1995). Second, many forms of acoustic communication are not the maximally loud calls typical of frog or insect mating calls, but are quiet or produced in an efficient range of the production mechanism. Thus, it is not surprising that actual empirical measurements indicate that the cost of signaling in birds and mammals are lower than for frogs ((Eberhardt, 1994; Vehrencamp et al., 1989) and often quite negligible for vocal displays ((McCarty, 1996; Chappell et al., 1995; Horn et al., 1995, Speakman, 1989 #3567; Speakman & Racey, 1991; Oberweger & Goller, 2001) see also (Gaunt et al., 1996)]. The costs of human speech are so low as to be nearly unmeasurable (Russell et al., 1998). Given the physiology of human speech this is not surprising: the motive power for speech is the elasticity of the lungs, which drives a stream of expired air that fuels vocal fold vibrations and the conversion of air flow into acoustic energy (Lieberman & Blumstein, 1988; Titze, 1994). Since air must be inspired into the lungs anyway to sustain life, the source of energy for speech is not a cost of vocalization, but part of resting metabolism (this may be another difference between mammals and frogs, which can respire through their skin - see (Fitch & Hauser, in press)). Thus, the physiological costs of spoken language are minimal, and quite unlikely to be a major factor in the evolution of spoken language or similar systems.

A second set of costs is worth mentioning: the neural cost of transmitting and processing information. The cost of acquiring information in the first place is not a cost of communication, but a cost of life. It is precisely the difference in cost between trial-and-error learning and signal-aided learning that is the main benefit of linguistic communication. Only the transmission of this information is truly a cost of communicating. To the extent that our large brains are necessary for language *per se*, not just to acquire

and remember the concepts language transmits, this physiological cost might be high, given the extreme metabolic activity of neural tissue, and the expense of creating it in the first place. However, this cost is so difficult to quantify given our current understanding of neurolinguistics that I can do little but mention it in passing. (Laughlin, 2001) gives an interesting analysis of the metabolic cost of information in fly vision.

A final set of costs that may be quite significant are associated with alerting unintended listeners to the caller's location. Nestling begging may alert predators to the location of the nest (Haskell, 1994), and vocal signals may also attract parasites or other unwanted guests (Webb et al., 1977). In the evolution of language, perhaps the most significant cost was due to unintended sharing of information with competitors. While the benefit of informing one's kin of the location of a new food source might be great, it could easily be offset if this also shared information with many unrelated competitors. To the extent that language has a cost, this seems likely to be the most significant, particularly if it is impossible to detect non-kin.

Earlier authors, starting with Darwin, have remarked on the possibility that sexual selection might lead to complex "displays" like those of human languages, by analogy with bird song. Mother tongues provide an alternative selective force that could underlie the generation of complexity: the need to communicate arbitrarily complex ideas. We can assume our common ancestor with chimpanzees had a complex conceptual store (of a sort that is present in chimpanzees and many other primates, including information about past events, distant locations, both transitory and permanent characteristics of individuals, etc.). In the mother tongue context, it is also reasonable to assume that much of this information would be valuable to offspring (or siblings, cousins, etc.) if it could somehow be transmitted to them. Thus, once a communication system of this sort was in place, each small increment of complexity (e.g., enlarged lexical capacity, speed of acquisition, or syntactic disambiguation) would correspond to an increment in the efficacy of information transmission, and thus inclusive fitness. The mother tongue hypothesis thus entails a selective force towards increasing complexity. The limits to which this selective force might push the system are determined again by Hamilton's equation, and as long as the costs are very low, even quite small and incremental benefits could be selected for (up to the theoretical limit of the complexity of conceptual structures of both communicators).

In contrast to sexual selection, the predictions of this kin selection theory for complexity fit quite nicely with the facts of human language competence. First, it is clear that mother tongues select for early competence on the part of offspring: the earlier a child's language competence comes on line the greater the benefit (both in immediate survival and in the sum of information transferable during childhood). Thus the remarkably early age at which children begin acquiring language, which is sharply discrepant with the predictions of sexual selection theory, makes perfect sense from the kin communication viewpoint. Second, given the primary role of females as caretakers, it is unsurprising that language abilities should be more developed in females than males. Of course, male children must communicate with their mothers, so we wouldn't expect mother tongues to be exclusively female.

Further, humans are unusual among primates in having a significant amount of paternal care, and thus adult male competence in language is also unsurprising (though if one sex was to selectively suffer language deficits, the theory predicts it would be males, as it is). Finally, the propensity of children to communicate among one another (particularly with siblings) is again predicted by kin communication but explicable only as a nonadaptive epiphenomenon by sexual selection theory.

The final implication of kin communication for the evolution of human language is the possible value of vocal imitation to indicate group membership, particularly kin group membership. Once a kinship based system for distributing favors arises, it is always susceptible to cheats who act like kin, receive benefits, but do not return the favor. This is known as the "free rider" problem, and has been extensively discussed ((Enquist & Leimar, 1993), see (Dunbar, 1996) for a review). I previously discussed imitation as a source of group-membership signals in general, which I abbreviate as "passwords" following (Feekes, 1982) in an earlier paper (Fitch, 2000). However, I don't think that this force is alone adequate for the level of detailed imitation seen in human speech. Something more is required than a simple shibboleth indicating membership in an arbitrarily formed social group. I join previous researchers (Nettle & Dunbar, 1997) in suggesting that an ever-changing dialect, mastered at an early age, could provide a reasonably reliable marker of distant kinship (it need not be perfect) and thus circumvent the free rider problem.

The basic idea here is quite simple: if offspring quite slavishly imitate the details of their parents (and perhaps siblings') pronunciation and grammar, and then cease imitating before "leaving home", they will be branded for life with a clue to their parental background. In the large fluid societies we live in today, with huge numbers of people in constant contact, this "brand" is called a regional and/or class dialect. In the much smaller, more closely-knit populations that characterized almost all of human evolution until 10,000 years ago, the information carried by a dialect would have been more specific, indicating at least the entire social group and probably giving cues to the specific kin group in which a child was raised. Later in life, individuals who could recognize their native dialect, and share information preferentially preferentially with those who spoke it, would be often be behaving preferentially to kin. Thus dialects could provide a means by which kin recognition could take place, boosting the power of kin selection. This could lead to either preferential exchange of information (in the lowest-cost case), and perhaps preferential exchange of other resources (food, shelter, coalitionary aid, etc.) as well.

A dialectal indicator of kinship is admittedly imperfect (unrelated orphans raised by the family would be treated as kin by this system), but this is no different from the various mechanisms of kin recognition known in animals (Hepper, 1991; Fletcher & Michener, 1987). For instance, mammal mothers typically learn to recognize their infants immediately after birth by their smell (Klopfer & Gamble, 1966), and can be duped into adopting a foreign infant by presenting it just after birth (Klopfer & Klopfer, 1968). Young birds typically come to recognize their parents, and own species, via imprinting (which can go awry when ethologists like Konrad Lorenz are the first organisms seen

(Bolhuis, 1991)). Birds often learn to recognize their species-specific egg pattern by examining their own first eggs, but if a cuckoo lays in this first nest they may be permanently confused. Mammals normally use proximity in early childhood as an indicator of kinship, refusing to mate with animals they were raised with (regardless of their actual genetic relationship) (Michener, 1974; Walters, 1987). This is probably true of humans as well, as illustrated by the fact that children raised together in a kibbutz do not marry. None of these systems are perfect, but all work well enough that their benefits overwhelm the occasional errors.

An animal example of such kinship calls may be the signature system of bottlenosed dolphins ((Sayigh et al., 1990), see also Tyack, this volume). Dolphins emit individual-specific frequency contours termed "signature whistles" which are constant through adult life and allow reliable identification of individuals. Dolphin calves start life by imitating the signature whistle of their mother. At puberty males emigrate away from their natal group, sometimes traveling hundreds of miles, and retain their mother's whistle throughout life. In contrast, females (who stay with their mothers as adults to form matriarchal kin groups) acquire a new whistle at adulthood. It is obvious that two strange males, encountering one another for the first time, could identify each other as brothers on the basis of their shared signature whistle. Given the propensity of male dolphins to form coalitions, this could increase their chances of forming kin coalitions (though no empirical data indicates that they actually do so). It is easy to see how such a system could also apply to nomadic hominids (male or female) who encountered each other for the first time, and immediately recognized each others' dialect as familiar.

By increasing the size of the kin group that can be preferentially communicated with, such a system of kin recognition would extend the kin group beyond the $r > 0.5$ of offspring, to include half-sibs, aunts and uncles, grandparents, half-cousins, etc. This expansion would also increase the store of information available to the speaker of a dialect. It is easy to see how this would both increase the value of the mother tongue in general, and put additional pressure for complexity and open-endedness on the system. Thus, if dialects are used to recognize kin, the communication system will be pressured to evolve the three key desiderata for human language: cheap honesty, slavish imitation, and generative complexity.

Conclusion

To summarize, I've argued that the most important characteristics of human language, the combination of which sets language apart from all other known communication systems, are explicable in the context of kin-selected communication systems, or mother tongues. This hypothesis is probably on the strongest footing in the case of cheap, honest communication. Abundant theoretical and empirical work suggests that cheap honesty is difficult to evolve among non-kin, but evolves easily and stably among kin. Indeed it is hard to see how selection would favor speech, the prototypical cheap, honest signal, among non-kin during the early evolution of language. Once a nascent system of kin communication has gotten started, and given a pre-existing set of complex concepts, mother tongues further provide a selective advantage for the communication of more detailed concepts, and thus for a highly generative system.

Finally, a kin-communication system will be made even more effective if it itself incorporates some clues to kinship and thus information exchange among a more extended set of kin than those immediately known to an individual. I suggest that the hyperaccurate ability of humans to acquire dialects provided such clues to kinship, which provides a positive feedback to the other aspects of kin communication described above, and explains why our imitation of dialects is far better than it need be for communication. Thus I think that the mother tongue hypothesis - that language developed primarily in a context of kin communication - provides both a good overall fit to much of the existing data, and a solution to some serious problems left standing by other models.

The advantage of this posited selective force over that of sexual selection which has been assumed by many earlier workers is two-fold. First, it accords with the facts that language learning begins in early childhood rather than at puberty, and second, it is expressed in both sexes rather than preferentially in males. The glaringly obvious flaw in this hypothesis is that today, language is not used exclusively or even predominantly to communicate among kin. Although I am uncomfortable taking refuge in the fact that current function and the function of the extant system need not be identical, I'm afraid this is necessary for now. The hypothesis predicts, however, that language should be used preferentially among kin in hunter/gatherer societies or other more traditional ways of human life. The third portion of the hypothesis also predicts that in such traditional settings, people should interact more favorably with those who share their dialect. Of course, no single hypothesized function will ever explain all aspects of human language. I have suggested, for example, that the descent of the human larynx may have originally been driven by selection to exaggerate body size, and only later been exapted for its use in expanding phonetic range ((Fitch & Reby, 2001; Fitch, in press)). Thus, I do not offer the mother tongue hypothesis as a total functional explanation, and indeed I doubt very much that such a holy grail exists. I do think, however, that the advantages of a kin-selected communication system for precisely those aspects of language that set it apart from other systems should be recognized and, I hope, further explored by others and incorporated into future theoretical treatments.

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