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Searching for Language Origins¹

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Abstract

Because language is one of the defining characteristics of the human condition, the origin of language constitutes one of the central and critical questions surrounding the evolution of our species. Principles of behavioral evolution derived from evolutionary biology place various constraints on the likely scenarios that should be entertained. The most important principle is that evolution proceeds by modifying pre-existing mechanisms whenever possible, rather than by creating whole new mechanisms from scratch. Another is that flexible non-genetic behavioral change drives, at each step, later genetic adaptation in the direction of that behavior. A model of language origins and evolution consistent with these principles suggests that increasing conceptual complexity of our ancestors—played out in the context of an increasingly socially interactive existence dominated by learned behavior—drove the elaboration of communications systems in our lineage. Empirical attempts to date the origin of important aspects of language hinge on key assumptions about how language and material culture are connected, or the relationships between anatomy, brain, and behavior. On the whole, the evidence suggests a very ancient origin of significantly enhanced communication, though exactly when this would have been identifiable to modern linguists as ‘language’ is unclear. It would appear that some critical components of language date back to the emergence of the genus *Homo*, with other component shaving an even deeper ancestry.

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1. This chapter has benefitted from numerous conversations over the years with Professor William S.-Y. Wang. I owe him a great debt of gratitude for his encouragement and support over the years, for the many opportunities he has afforded me to interact with such interesting scholars in a number of conferences and workshops he has organized, and for his keen interest in language evolution. His breadth of interests, his recognition of the many sources of potential knowledge on topics about language evolution, and his deep understanding of the issues, are things I have always admired. This chapter has also benefitted from conversations with Vincent Sarich, Morten Christiansen, Robert Port, Robert Seyfarth, Dorothy Cheney, James Hurford, Tao Gong, JinyunKe, Thomas Lee, Craig Martell, James Minett, Ching Pong Au, Feng Wang, and Reina Wong. I also wish to thank Shi Feng and Peng Gang for organizing this Festschrift for Professor Wang, and for their patience.

1. Introduction

The key to the evolution of language also lies far away from us—lost in the dim and remote past of man's earliest developments. When we consider the nature of the challenge, we should, of course, be fully aware of the magnitude of the task. However, it is a key well worth the search, because there is no more critical achievement of the human mind than the invention of language. The more deeply our search takes us into the nature and development of this invention, the more we have come to appreciate the magnificence of this achievement (Wang 1991, 131).

The unique place that humans hold in the evolution of life is in large part the result of the advent of language. The depth and complexity of the types of things about which humans are able to communicate have allowed for a level of coordination, elaboration of shared knowledge, and richness of social life that appear to exceed that of any other species. Reconstructing the origin and evolution of language is therefore one of the most interesting questions not just for linguistics, but for the entire field of evolutionary biology as well.

Professor William Wang has long recognized the importance of this question, and has encouraged many others to this goal through his own thoughtful research and writing. The present author was one of those inspired to pursue this 'holy grail' of evolutionary questions, having first read Professor Wang's essay "Exploration in language evolution" (Wang 1991) as a graduate student. The present essay is an attempt to follow in his footsteps, outlining some of the paths that have been pursued to try to illuminate the natural history of language.

While it is clear that the capacity for language rests upon biological foundations, it is the fact that it is culturally transmitted that endows it with its immense potential for elaboration and adaptation (Wang 1991, 108–109)

The fact that the phenomenon of human language has both biological and learned cultural dimensions means that an understanding of its origins and evolution requires an integrative, biocultural approach. It is sometimes suggested that the cultural evolution of language is independent of its biological evolution (e.g., Croft 2000). However, the cultural evolution of language is in fact the driving force behind its biological evolution. The recognition that cultural evolution is much faster than biological evolution has led to the suggestion that language adapted to the human brain more often than the human brain adapted to make language possible (Christiansen 1994; Christiansen and Chater 2008; Deacon 1997). Understanding the cultural evolution of language, and especially how it is used by individuals as part of their social existence, is therefore critical to understanding the evolution of language in the broad sense.

2. Evolutionary Principles

An analysis grounded in an evolutionary perspective makes a set of predictions about how behavioral evolution—of any kind—is likely to proceed. These predictions stem directly from a set of basic principles central to evolutionary biology. The most important of these is that,

whenever change occurs, evolution proceeds by modifying pre-existing mechanisms, rather than by creating whole new mechanisms completely from scratch. This is because complex, directional, evolutionary change must in all cases be reproductively adaptive within each and every generation. This in turn rewards individuals who push the limits of their own pre-existing cognitive machinery in order to approximate some behavioral ability. If it were possible to change instantly from completely lacking any of the cognitive machinery necessary for communication, to having full-blown complex natural human language, then it would be possible to take seriously the idea that human language is cognitively unique and shares no common circuitry with any non-human animals. However, it seems very clear that no such single macro-mutation could possibly explain the appearance of language, given the widespread and varied brain resources that are required for language (see e.g., Schoenemann 2009a). Some language theorists have maintained that at least some key aspects of human language are likely to be unique—not deriving from any pre-existing circuitry (Chomsky 1972; Hauser et al. 2002; Pinker 1994). From an evolutionary perspective, however, this is almost surely false, with its likelihood being inversely proportional to the complexity of the supposedly unique features (the more complex, the less likely the features are truly unique). Thus, we must take seriously the idea that meaningful continuities exist between human and non-human communication and cognition.

The ubiquity of preadaptation has a corollary, which is that flexible, non-genetic behavioral change will drive, at each step, later genetic adaptation in the direction of that behavior. If it is beneficial for an individual organism in a particular environment to adapt to new social conditions in some way, this organism must, by definition, do so through the use of behavioral patterns that are not hard-wired. Such a process, repeated generation after generation, will result in evolutionary (genetic) change being driven by behavioral change, and not the other way around. Within evolutionary biology, behavioral change is understood to be the primary driver of many key events in the evolution of life (Lieberman 1984; Mayr 1978). There are numerous examples in human evolution itself, even aside from language, that demonstrate this quite clearly (Schoenemann 2010a). It is now understood that selection favored the evolution of sickle-cell in some African populations because heterozygotes are protected against malaria (Friedman and Trager 1981). It turns out that malaria itself has inadvertently been spread through human behavior, because agriculture creates prime environments for the parasite. Thus, the spread of agriculture (a cultural/behavioral change) drove biological adaptation in the form of sickle-cell (Livingstone 1958).

Another example can be seen in the biological adaptations that allow for the drinking of milk as adults in some European and African populations. Among mammals generally—and the majority of human populations today—adults are actually lactose-intolerant (i.e., unable to digest the major sugar in milk). The few human populations that can drink milk today all have a long history of domestication of animals that were able to produce significant quantities of milk. Because the ancestral condition among humans was to be lactose intolerant as adults, the initial domestication would not have been for milk, but rather for meat and/or hide. It was only after domestication for other reasons that selection could favor genetic changes that allow for adult milk consumption (Durham 1991).

The transition to bipedalism—another critical adaptive shift in human evolution—was also driven by behavioral changes. Hominins did not evolve efficient bipedal anatomy first, only to

stumble upon its usefulness later. Instead, there was an adaptive benefit in early hominin niches for bipedalism, if it could somehow be accomplished. Apes today can walk bipedally, though with significantly more difficulty than humans. Thus, individual hominins who could spend longer and longer periods bipedal would have had reproductive benefits over those who could not. The behavioral shifts towards increasing bipedalism would have driven the selection for more efficient bipedal anatomy (see e.g., Hunt 1994).

Exactly the same kind of process would have occurred with respect to language evolution: It must have been beneficial for individuals to communicate with others in their social group, in an increasingly sophisticated manner. Thus, individuals who were able to use whatever pre-existing cognitive mechanisms were available (to themselves and others) to communicate as effectively as possible, would have had the greatest adaptive benefits. Evolutionary changes enhancing language abilities in such a process would have been biased towards modifying these pre-existing abilities at each and every step of the evolutionary process. This does not lead to the evolution of unique modules specific only to language, but rather with obviously modified circuits that show clear evidence of modifications from non-language circuits. We should expect to find minimal biological changes, and should therefore look for ways in which we might explain language in these terms.

Another key part of the story derives from the recognition of the fundamentally interactive nature of communication. As Wang (1991) pointed out, language by definition requires both a sender and a receiver. In order for any new language-relevant mutation to be adaptive for a sender, other individuals in the social group must already have the cognitive circuitry that allowed them to understand the enhanced communication made possible by this mutation. Similarly, in order for a new mutation to be adaptive for a receiver, other individuals must already be producing the types of enhanced signals that could take advantage of such mutations. In both cases, adaptive change would have occurred towards features that either benefited greater understanding of others (given their pre-existing cognitive abilities), or greater understanding to others (Schoenemann 2009b). The types of mutations that would fit these constraints would necessarily be slight modifications of existing cognitive circuitry, not wholly new circuits.

3. Preadaptations

Language evolution presupposed a rich social existence, thereby making enhanced communication adaptive. Primates are particularly social animals, and are social in a way that is intrinsically interactive and not simply the result of a passive, 'safety-in-numbers' survival strategy. Communication is implicit to this kind of interactive sociality: it is difficult to imagine interactive social interactions devoid of some form of communication. Thus, primate sociality was a critical preadaptation to language. Humans appear to have further elaborated this degree of sociality to an extreme (Dunbar 2003) (see below). All of this further presupposes that there were useful things to learn from others, or useful things to communicate to them, which in turn requires that there be a rich enough internal conceptual world in individuals such that, ultimately,

it could be useful to code this information in some manner symbolically. What evidence exists of conceptual understanding in primates? Perhaps the most obvious evidence derives from studies of alarm calls for different predators that have been documented in at least three different monkey species (Cheney and Seyfarth 1990; Zuberbuhler 2000), and at least one gibbon species (Clarke et al. 2006). In order for these primate species to have such calls, they must have separate concepts for each type of predator.

The complexity of their conceptual understanding is not limited to a handful of different predators, however. Baboons at least have been shown to recognize hierarchical relationships both at the level of individuals and families within their social groups (Bergman et al. 2003). This means that individual baboons actually know a great deal of detailed social information about their group (Seyfarth and Cheney 2003). Though there is no evidence that they code this information in some form of productive vocal communication system, they certainly act on this information, indicating that they must have the underlying conceptual understanding of these relationships.

In addition to this, a plethora of ape language studies have demonstrated that, at the very least, apes can learn arbitrary signs for a wide variety of different concepts (Gardner and Gardner 1984; Premack and Premack 1972; Savage-Rumbaugh et al. 1993). This means they must have conceptual categories sufficiently distinct to allow them to mark these reliably with arbitrary symbols. Thus, the conceptual foundations of language would appear to have been set long prior to language evolution. This would, in fact, have to have been the case, because it would not make sense for our ancestors to evolve language if they had nothing to communicate about (Schoenemann 1999).

The use of combinatorial rules (precursors of syntactic rules) in non-human primate communication systems has been much harder to demonstrate, but some intriguing findings have been reported. Campbell's monkeys (*Cercopithecus campbelli*) have been reported to produce the equivalent of a "not" signal in front of their normal predator alarm calls to indicate something akin to: "not a leopard" (Zuberbuhler 2002). In gibbons, their predatory-induced songs apparently differ from their regular songs not in the specific notes used, but rather in how they were specifically organized into songs, and these organizational differences appear to be meaningful to other conspecifics (Clarke et al. 2006). Among ape language studies, Kanzi appears to understand simple grammatical constructions in spoken English, distinguishing above chance commands like: "put the ball on the pine needles" from "put the pine needles on the ball", as well as: "take the ball outside" from "get the ball that's outside" (Savage-Rumbaugh et al. 1993; Savage-Rumbaugh et al. 2009). To do this, he must understand, at least at a rudimentary level, some of the completely arbitrary symbolic features of English grammar—for example that sequential order codes features of argument structure (what gets done to what).

All of this suggests that the following basic components essential to human language were in place long before the human lineage split from the great apes: (i) the existence of distinct cognitive concepts that could be (ii) coded with arbitrary vocalizations, (iii) the incipient ability to use a completely arbitrary device (sequential order) to mark argument relationships between concepts, and (iv) the ability to use these for communicative purposes.

4. Evidence of Language Origins

The determination of when language began depends entirely on what one means by “language” (Wang 1991). If one imagines language evolution as a continuous progressive development, then there is no specific point in time where language could be said to have appeared. Wang (1991) likens it to asking when a man who has been losing his hair finally becomes bald. Models of language evolution emphasizing distinct intermediate stages, on the other hand (e.g., Bickerton 1995), posit more clear cut transitions between key language developments, which presumably would be more clearly marked in the evolutionary record.

The extent to which language evolution was continuous vs. discontinuous is not actually clear. The spread of new features across languages does appear to occur nonlinearly, following an approximate ‘S’-shaped curve (Shen 1997; Wang et al. 2004). Computational models of language change/evolution also often display relatively sharp transitions between states (Gong et al. 2005; Ke and Holland 2006). However, even if we assume individual features of language changed non-linearly, it is still possible that overall language evolution was relatively continuous, if we assume that the change in individual features were independent of each other, and therefore spread over time with different starting points. It is probably most relevant to approach the question of language origins from the perspective of changes in communicative efficacy, rather than the presence or absence of specific grammatical features. From this point of view, language change was arguably continuous.

What direct evidence is there for the origin of language? Because language behavior itself does not fossilize, language evolution must be inferred either from its effects on fossil skeletal anatomy and/or from the material culture left behind by our distant ancestors. A number of theorists have argued that the evidence points to fully modern syntactic language occurring relatively late in human evolution, coincident with—or subsequent to—the origin of our own species, *Homo sapiens* (Bickerton 1995; Klein and Edgar 2002; Tattersall 1998). This would date the origin of language to somewhere under ~150,000 years ago. By contrast, others would prefer to push the date of language origins substantially further back, to more than ~500,000 years ago, and perhaps as far back as the origin of our genus ~2 million years ago (Dunbar 2003; Laitman 1985; Schoenemann 2005; Tobias and Campbell 1981). As will be discussed, it is possible these divergent views are focusing on different parts of the whole story of language evolution, and that neither is actually wrong, but instead both are true but incomplete by themselves. Each may be looking at different parts of a complex evolutionary history.

4.1 Evidence consistent with a recent origin

One of the central arguments offered for a recent development of language is the significant increase in the complexity and range of material culture, particularly in artistic expression, which show a rather dramatic increase in occurrence by ~35,000 years ago. Evidence of even earlier art appears in places in Africa, such as at Blombos Cave in South Africa, where pigment (ochre) processing materials were recently found, dating to ~100,000 years ago (Henshilwood

et al. 2011). The connection of representational art specifically to language is tenuous, however. For one thing, representational art is not direct evidence of the type of symbolic activity that is central to language. Linguistic symbols have arbitrary connections with their referents, whereas representational art directly reflects the referent in some obvious way. In the terminology of Pierce (1867), words are true symbols, whereas objects of representational art are just likenesses (he later used the term ‘icon’; see also Fetzer 1988). Direct evidence of language would instead require something resembling writing rather than just art. Writing, however, appears to have taken tens of thousands more years to develop. When it does occur, it appears concurrent with very large increases in population, spurred by resource surpluses resulting from the development of agriculture. The first writing systems appear to have been essentially accounting tools (Schmandt-Besserat 1991). Thus, even if we assume that the flowering of representational art marked the origin of language (or at least fully modern syntactic language), actual direct evidence of language would not occur until much later. It is not clear how confident we can be that representational art—as opposed to other possible markers to be discussed below—specifically marks the origin of language. Representational art indicated an enhanced interest in thinking about past events, but its direct connection to language is tenuous.

Henshilwood and Marean (2003) suggest that evidence of non-utilitarian material culture, even if not representational art itself, is nevertheless suggestive of language: “Decoding the meaning of a design engraved on a piece of ochre or understanding why a bone tool is crafted much more carefully than necessary for a utilitarian object is difficult, but objects like these are strongly suggestive of the advanced levels of symbolic thought and language that were necessary for the development of modern behavior” (p. 636). Exactly why language would be required to create engraved designs, or particularly carefully crafted tools, is not clear however. Furthermore, while language may or may not be necessary for such apparently non-utilitarian material culture, it doesn’t follow that language must have originated at the same time as the earliest archaeological evidence of such culture. As Glynn Isaac (1976) has pointed out, “lack of elaboration does not prove lack of capability.” At best, evidence of non-utilitarian material culture would simply suggest that language had fully emerged by ~100,000 years ago.

Another problem with the attempt to tie art to language involves the recognition that there exists among living peoples—all of whom have fully modern language—a huge range of variation in complexity of material culture. The differences between modern cultures in this regard cannot be due to presence or absence of symbolic language, or of specialized evolved circuits in different populations, and are instead a function of population density and accidents of history. As Glynn Isaac (1976) noted when discussing the degree of complexity of stone tool assemblages in the archaeological record:

Few, if any, of the assemblages have ever approached in complexity the limits of capability of their makers. Even the complex material culture of modern times has not presumably reached the extremes of which mankind is capable...If we look at ethnographic information on the artifacts of recent nonagricultural peoples, we find great differences in the degree of elaboration as measured in various ways, in spite of the fact that inherent capabilities are not known to differ. (p. 277)

Complexity in material culture lags behind cognitive evolution. Because the flowering of art in the Upper Paleolithic is also coincident with the development of a wide range of advancements in tools and technology (Schick and Toth 1993), it is entirely possible that the appearance of art simply marks the development of advanced technology (itself likely the result of an earlier increase in population density). The earliest evidence of art is not an unequivocal marker for the origin of language.

Furthermore, there are strong suggestions of artistic endeavors going back much further than even the 100,000 year old date for Blombos Cave material. The collection of fossils by hominins appears to have occurred long before this (Oakley 1973). In a few cases, handaxes dating to ~200,000 years ago have been found with fossil shells prominently centered in their side views, possibly intentionally (Figure 13.1; Oakley 1981). The Paleolithic site of Terra Amata in France, which appears to be even older, revealed several pieces of red ochre that appeared to have been extensively worn through use (de Lumley 1969), presumably as pigment. If the advent of art does indeed signal the origin of language, and if these early examples represent incipient artistic expression as they appear to, then language origins would predate *Homo sapiens*.

Figure 13.1 ~200,000 year old Handaxe from West Tofts, England, containing a beautiful fossil shell in the center

Photo courtesy of the Museum of Archaeology and Anthropology, University of Cambridge.



Additional indirect arguments for a recent origin of language have been proposed on the basis of anatomical considerations of fossil specimens. In one case, the narrowness of the thoracic vertebral canal of a particularly complete *Homo erectus* specimen (KNM-WT 15000) has been used to suggest that that species (which predated *Homo sapiens* and even Neanderthal) lacked language (Walker and Shipman 1996). The vertebral canal transmits the spinal cord, and in the thoracic region carries the nerves that innervate the intercostal (rib) muscles of the chest cavity. Since language is partly dependent on the intricate maintenance and manipulation of air pressure through the larynx, and assuming that the size of the vertebral canal accurately predicts the degree of sophistication of muscle control in the chest, Walker and Shipman (1996) argue that narrowness of the vertebral canal could be a marker for language. This conclusion has been called into question, however, by suggestions that KNM-WT 15000 is actually just pathological with respect to its vertebral canal (Latimer and Ohman 2001). This is further supported by that fact that more recent *Homo erectus* specimens from the site of Dmanisi in the Republic of Georgia, show normal (for modern humans) vertebral canal dimensions (Meyer 2005). In addition, it is not clear that intercostal muscles actually play a significant role in vocal production to begin with (Meyer 2003).

Another line of fossil anatomical research relevant to language origins has focused on the position of the larynx, which is much lower in the neck in modern humans than it is in apes. Lieberman (1984) argues this allows for a wider range of vowel sounds in humans, and furthermore would not have evolved unless it had some important benefits because it should be expected to increase the likelihood of choking on food. Although choking appears to be very rare in modern humans (Clegg and Aiello 2000), very weak selection can still result in very large evolutionary effects (Schoenemann et al. 2000). Fitch and Reby (2001) point out that red-deer also have descended larynges, which they argue is used for sexual-selection purposes, to make themselves appear larger than really are. They argue that this calls into question the idea that our descended larynx is specifically due to its usefulness for language. However, for this argument to hold, we would have to believe that sexual selection would have been stronger in hominins than all other primate lineages, since only humans have descended larynges among primates. However this is highly questionable: gorillas and orangutans display much greater sexual dimorphism than do humans (Alexander et al. 1979), yet do not show descended larynges.

The extent to which the actual range of sounds is critical to fully modern language is also unclear. Only a handful of distinctive sounds (phonemes) are required to create an infinite number of words, because it is the sequential patterns of sets of sounds that create distinct words, not the individual sounds themselves. The number of phonemes used in specific languages ranges widely (Wang 1976), with Hawaiian making use of only perhaps 15. In addition, the position of the larynx only affects vowel sounds—not consonants—and therefore only influences a relatively small subset of the total phonemes available. Thus, larynx position is likely not a limiting factor with respect to language evolution, though increasing range of vowel repertoire, when it does occur, would presumably say something about the increasing use of vocalizations over time. Larynx position should lag the development of language, not clearly mark its origins.

Estimating the location of the larynx in specific fossil specimens is difficult, because the larynx itself is cartilage and does not fossilize, and the hyoid bone that it hangs on does not have bony attachments to either the cranium or the vertebral column. One method used to infer

its location has been to assess the amount of downward flex evident in the posterior part of the bottom of the cranium. The greater the degree of flexion in the cranial base, the lower the larynx is assumed to be. This method has been criticized on anatomical grounds (Arensburg et al. 1990; Burr 1976; Falk 1975), but it does appear that the cranial base is significantly more flexed in modern humans than in modern apes, and this likely has at least some affect on vocalization. Applications of this method suggests that Neanderthal (~130–30 KYA) did not have larynges as low as adult modern humans (Laitman et al. 1979). However, the multivariate analysis actually groups Neanderthal specimens closer to sub-adult modern human children than it does to apes. As an example, one classic Neanderthal specimen from the site of La Ferrassie in France groups most closely with 6–18 year old modern human children (not apes of any age). When talking to a child even as young as 6 years old, it is easy to convince one's self that their phonetic abilities are not meaningfully restricted with respect to their ability to use language. If cranial base flexion is actually telling us something about the location of the larynx, and therefore about the range of linguistic sounds that a fossil specimen was capable of, then we must conclude that even Neanderthal had the ability to make a sufficiently wide range of sounds to approximate that found in modern human children. Unless we have a principled reason to exclude modern human children from possessing modern human language, this research actually supports a much more ancient origin of language. Lieberman (1984) himself, in fact, specifically states he is "...not claiming that Neanderthal hominids lacked language and culture..." (p. 322).

It is important to note here that those who argue for a relatively recent origin for language tend to focus not on language as a whole, but rather only on specific aspects—subcomponents—of modern language that they believe are critical, such as the development of syntax (e.g., Bickerton 1995) and/or the full range of sounds utilized by different modern languages (e.g., Lieberman 1984), rather than thinking about language as a complete package. By focusing on subcomponents they actually implicitly acknowledge that some form of enhanced symbolic communication would have been evident long before the emergence of fully modern language. Exactly what the difference was between earlier and later linguistic forms depends on the theorist. For Bickerton (1995), earlier communication systems—which he refers to as “proto-language”—lacked syntax and grammar entirely. By contrast Lieberman's (1984) emphasis has been on the evolution of phonological abilities. But for both of these models, any proposed tight, functional linkage between art and modern linguistic abilities should be seen as tenuous at best. Such ideas seem to be based more on a simplistic desire to tie together in one neat evolutionary package key behaviors thought to be particularly distinctive to modern humans. It is entirely possible that different key types of behavior occurred at different times during human evolution. The origin of bipedalism in our lineage predated the dramatic increase in brain size by at least a million years (and probably more) is one well-understood example. Why exactly art would require fully syntactic language, and why the appearance of art should indicate something more about language than about important human demographic changes, for example, is not clear. It is likely a mistake to privilege one aspect of language over others as being more crucial to its evolution. The roots of language appear to extend very far back, long predating *Homo sapiens* as a species.

4.1 Evidence Consistent with an Ancient Origin

There are a number of lines of evidence that directly hint at a much older origin of language. One source of evidence ironically stems from the same cranial base flexion work discussed above, which had been used to suggest that Neanderthals lacked the same range of sounds as that found in adult modern humans. Laitman (1983) and colleagues' work has shown that Middle Pleistocene hominins from Steinheim and Broken Hill, which predate Neanderthal (and are likely transitional forms deriving from even older *Homo erectus*), actually show the same degree of flexion that is found in modern humans. In fact, Laitman argues his analysis shows that the lowering of the larynx had progressed significantly beyond the ape condition even as far back as *Homo erectus*, which he believes therefore "...had made a quantum step toward the acquisition of the full range of human speech sounds," (Laitman 1983, 83). The oldest hominid specimen examined by Laitman and colleagues that appears to be significantly different from the ancestral ape condition in this regard is OH 24, a *Homo habilis* specimen dating to ~ 1.8 million years ago (Laitman 1985; Laitman and Heimbuch 1982; Lieberman 1984). Thus, to the extent that cranial base flexion does indicate something about the position of the larynx, and is therefore marking something important about language, it actually suggests that—at a minimum —significantly increased vocal communication goes back to the earliest *Homo* lineages.

A study by Duchin (1990) came to the same conclusion using a different set of anatomical relationships. Duchin (1990) estimated the location of the larynx through its relationship to the hyoid bone, using discriminant function analysis. She was able to predict hyoid location from the length of the mandible and palate in modern chimpanzees (*Pan troglodytes*) and humans. Measurements from both a *Homo erectus* and a Neanderthal specimen, when entered into the discriminant function equation, unequivocally grouped these fossils within the modern human range, and not with chimpanzees

Although the hyoid itself is rare in the fossil record, one Neanderthal specimen has been found, from the site of Kebara in Israel. Analysis suggests that this hyoid is essentially the same as those of modern humans (Arensburg et al. 1990). It is not known, however, how well hyoid shape itself predicts the range of vocal sounds possible for an individual, which makes the relevance of this find to the present discussion unclear.

Other suggestive evidence for a very old origin of language comes from studies of the endocasts (inside surfaces of brain cases) of early hominins. One focus for language evolution has been an area called Broca's cap. This is an indentation on the interior surface of the brain case (resulting in a protrusion of the endocast) at a location that overlays Broca's area of the brain. Broca's area in modern humans plays a key role in language production, including an important role in processing both aspects of syntax and semantics (Bear et al. 2007; Damasio and Damasio 1992; Posner and Raichle 1994). Studies going back to Broca himself (1861) have demonstrated a lateralization of language production to the left hemisphere for most subjects. This functional lateralization also appears to be reflected in actual morphological differences between left and right hemispheres in the size of Broca's area itself (Albanese et al. 1989; Falzi et al. 1982; Foundas et al. 1996). Because homologs of Broca's area have been found in the brains of apes and even monkeys (Striedter 2005), it is reasonable to assume that Broca's caps on

hominin endocasts reflect something about the underlying Broca's area region of the individual. However, because apes and monkeys lack human language, the simple presence of Broca's area itself is of course not a reliable marker of the presence of language. There is some evidence that apes have morphological asymmetries in the brain as well in the region of Broca's area favoring the left hemisphere (Cantalupo and Hopkins 2001), however this study only assessed surface area extent in corresponding hemispheres (which would not necessarily be obvious on fossil endocasts). A study of the actual endocranial surfaces of modern apes and humans using non-rigid deformation analysis suggested that humans do have greater asymmetry in the region of Broca's cap (Figure 13.2; Schoenemann et al. 2008). All of this suggests that the endocranial morphology in the region of Broca's cap of fossil hominins is relevant to origins of language.

Fossil endocasts often, unfortunately, do not retain clear morphological signals of the underlying brain. However, one early *Homospecimen* (~1.8 million years old): KNM-ER 1470 (usually classified as *Homo habilis*), appears to have a more human-like brain surface morphology (pattern of gyri and sulci) in the region of Broca's cap (Falk 1983). This is certainly suggestive of a very early development of language, though does not prove it. Other early *Homo endocasts* generally cannot be assessed in the same way, however, either because of the relevant area is missing or the morphology is unclear in that region.

However, it is possible to at least assess the relative asymmetry in the size of Broca's cap for a fair number of fossil specimens. Holloway et al.'s (2004) compendium of hominin endocasts includes an assessment of Broca's cap asymmetry for all specimens in which both left and right sides are represented. Their assessments show that of the 19 hominin specimens (17 *Homo* and 2 *Australopithecine*) for which Broca's cap asymmetry can be assessed, all but two demonstrated obvious left-biased protrusion of Broca's cap. Figure 13.3 plots these specimens by age and cranial capacity. As can be seen, the only two right-biased specimens are relatively recent, and happen to be Neanderthal specimens. Brain size also appears to be unrelated to degree of hemispheric asymmetry in this region. While these asymmetries do not prove that early hominins had language, they are highly suggestive of neurological changes relevant to language.

An additional attempt to assess the time course of language evolution in fossils involves the assessment of changes in the size of the opening through the cranium that carries most of the nerves that control the tongue: the hypoglossal canal. The relevance to language is that the movement and placement of the tongue plays a critical role in forming the sounds used in speech (Denes and Pinson 1963). Kay et al. (1998) showed that humans average larger hypoglossal canals than do apes, as well as that a handful of hominin specimens they were able to assess fell closer to the human average than ape average. The oldest hominin in their sample was the Kabwe *Homo heidelbergensis* specimen (thought to be ~200,000 years old). This study was questioned by DeGusta et al. (1999) who measured a larger set of human specimens and also included a sample of the small-bodied apes (gibbons) and several other non-ape primates. They reported a much greater overlap with all the apes (which this time included the small-bodied ones). They also presented data from a small study of 5 cadaver specimens suggesting canal size was not unequivocally related to hypoglossal nerve size. From this they argued that hypoglossal canal size was not appropriate for inferring the presence of language. However, even using their broader comparative sample, Kabwe still had a larger hypoglossal canal than any of their ape

Figure 13.2 Asymmetry in endocranial morphology at Broca's cap

Left hemispheres of: A. Human (*Homo sapiens*), B. Bonobo (*Pan paniscus*), C. Chimpanzee (*Pan troglodytes*). The ovals indicate the approximate region of Broca's cap for each species. Shading indicates degree of difference between the hemispheres, with darker indicating greater protrusion for left vs. right. Greater dark shading within the human oval compared to the other species therefore indicates greater left-biased asymmetry in humans. Analysis from Schoenemann et al. (2008)

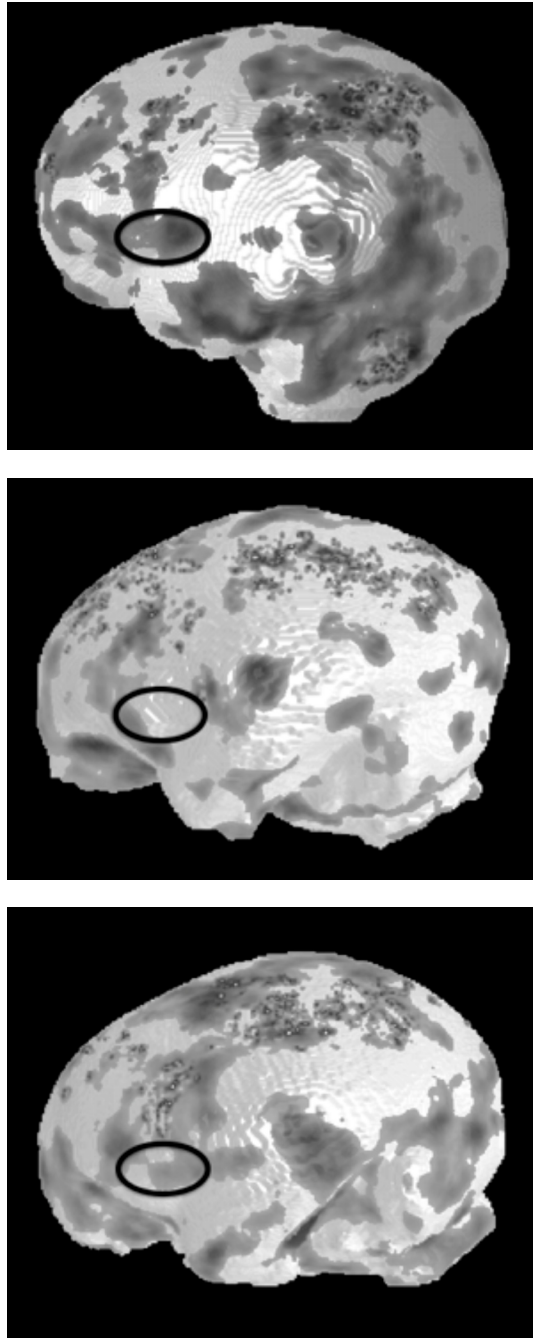
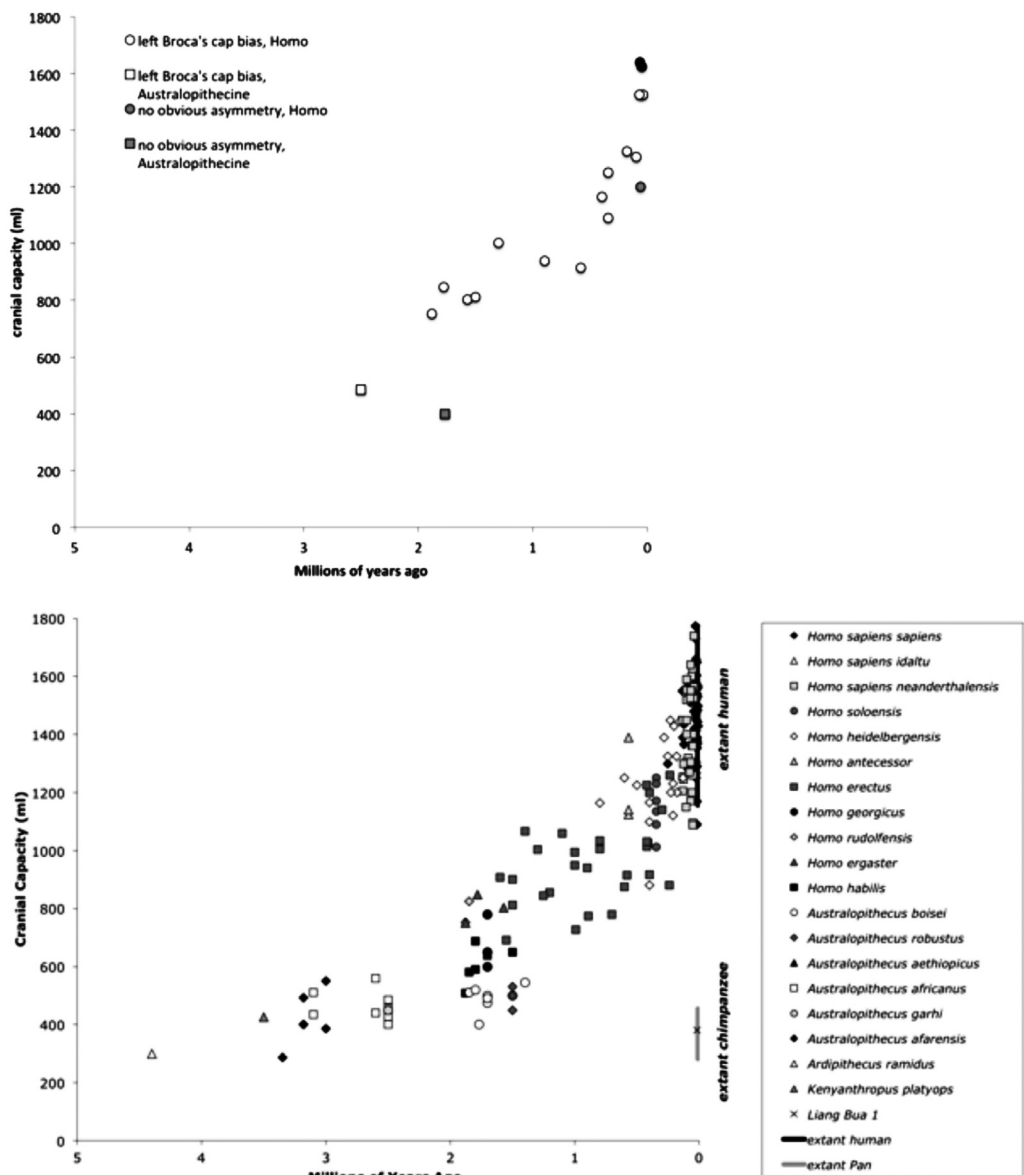


Figure 13.3 Evolution of hominin endocrania over time

A. Asymmetries in Broca's cap in fossil hominins. Specimens are plotted by estimated age and cranial capacity. Circles indicate presumed Homo specimens; squares indicate Australopithecine specimens (more distantly related Hominins). White shading indicates left greater than right; gray shading indicates no obvious difference between hemispheres; black shading indicates right greater than left. Fossil asymmetry assessments for Broca's cap are from Holloway et al. (2004). B. Cranial capacity of all hominin specimens. Specimens are plotted by age and cranial capacity, with presumed fossil species indicated. Modern human and chimpanzee ranges are shown for comparison. Cranial capacity of Homo specimens, which date back almost 2 million years, exceed that of modern chimpanzees, whereas Australopithecines overlap. Data sources compiled from the literature by Schoenemann (in press).



specimens, and the two Neanderthal specimens in their study were larger than all but the very largest 2 ape specimens (which were likely very large bodied gorillas, though it is not clear from their tables). Thus, though this data is equivocal, it is nevertheless suggestive of increased hypoglossal canal size in hominins, and therefore is consistent with the emergence of increased vocalization at least back to *Homo heidelbergensis* (measurements for older hominins have not been reported to date).

One additional intriguing piece of evidence consistent with an older origin of language is that reconstructed Neanderthal DNA reportedly shows the modern human variant of the FOXP2 gene (Krause et al. 2007). This gene has been implicated in language evolution because mutations of it appear to severely affect language production. Although early claims suggested that FOXP2 might be grammar specific (Gopnik and Crago 1991), individuals with the mutation have a range of impairments, including verbal IQ 19 points lower on average than non-affected family members, pronounced impairment in articulation, and difficulty copying arbitrary or ofacial sequences (Vargha-Khadem et al. 1995). Furthermore, their linguistic deficits with respect to grammar involve a type of morphosyntax that is not universal, and hence cannot be a part of so-called “Universal Grammar” (Schoenemann and Wang 1996). Nevertheless, it has been under apparent selection specifically in the human lineage (Enard et al. 2002), and is likely relevant to language evolution. The finding that the modern human variant was apparently shared with Neanderthal suggests this variant predated the supposed Neanderthal/anatomically-modern-human split. As this has been estimated to be greater than ~300,000 years ago, this would be further evidence of a deep ancestry of important aspects of language.

Lastly, an argument can be made that brain size itself is a reasonable proxy for important parts of language evolution. First, it has been shown that brain size is correlated with a wide variety of markers of increased social complexity, including average group size (Dunbar 2003; Sawaguchi 1988; Sawaguchi 1990; Sawaguchi and Kudo 1990) and the incidence of apparent acts of deception (Byrne and Corp 2004). This therefore suggests that the dramatic increase in brain size in the human lineage, evident by ~2 million years ago (Figure 13.3B), likely involved a significant—and increasing—rise in the extent of social interactivity among hominins. Given that this occurred in the context of the already intensively interactive social existence among primates generally, which is intrinsically communicative in nature to begin with, it is difficult to see how these additional increases could have occurred without involving some form of significantly enhanced communication (c.f., Dunbar 1996). Intriguingly, it has recently been shown that brain size is a significant predictor of the size of the reported vocalization repertoire in primates—even independent of social group size (Hurst 2011).

In addition to this, a major cognitive effect of the brain size increase in hominins was almost surely a very large increase in the complexity of conceptual understanding and awareness (Schoenemann 2005; Schoenemann 2010b). This inference is grounded in the idea that conceptual understanding is instantiated in the brain as networks of interconnectivity between specialized processing regions (Barsalou 2010). Since increasing brain size appears to lead to *decreasing* levels of overall broad connectivity between existing regions (Ringo 1991), larger brains inevitably contain regions that are less directly interconnected than are smaller brains. Because they are less directly interconnected, there is a greater degree of independent

and distinct processing within particular regions. In addition, larger brains empirically tend to have larger numbers of distinct anatomical regions (Changizi and Shimojo 2005). Although the specific functions are not always known, these anatomical distinctions are presumed to indicate functional distinctions as well. Thus, larger brains not only have more distinct regions, but these regions are also increasingly distinct with respect to the processing they carry out. Given that concepts are built upon networks of activation among different regions, a larger number of distinct regions will lead to an increasingly rich conceptualization of the world. This means that they would have increasingly interesting things to communicate with others in their social group. This would go hand-in-hand with the increasingly intense, socially-interactive (i.e., communicative) existence of primates, leading inevitably to increasingly complex communication.

Exactly at what point during this process one could label this enhanced communication a true “language” depends, as pointed out before, on exactly what one believes language entails. For many, a language is a communication system that has grammar and syntax (Bickerton 1995; Jackendoff 2002; Pinker 1994). The enhanced communication implied by early hominin brain size increase ~2 million years ago may not have involved syntactic devices sophisticated enough for these theorists to accept the label of “language.” However, the degree to which grammar and syntax are truly evolutionarily and cognitively independent of conceptual understanding is highly debatable. There are several models of language that argue grammar and syntax cannot be understood independent of semantics (Haiman 1985; Langacker 1987; O’Grady 1987). To the extent something like these models is true, evolutionary elaboration of the conceptual system (as estimated by increasing brain size) would then be a valid proxy for the development of grammar.

Furthermore, the extent to which there actually are any universals of grammar, and therefore evidence for uniquely evolved separate neural circuitry for grammar, has been seriously questioned (Evans and Levinson 2009). It has been pointed out that grammatical and syntactic features of language that have been claimed to be universal (e.g., Pinker and Bloom 1990) are remarkably general, and instead look very much like simple reflections of our conceptual understanding of the world, rather than rules independent of meaning (Schoenemann 1999). This calls into question the extent to which grammar is really distinct from conceptual understanding, rather than just being an emergent cultural manifestation of it. Savage-Rumbaugh and Rumbaugh (1993) suggest modern human grammatical abilities would likely have been built up in this way, based upon the basic abilities they and others have demonstrated for modern apes. All of this undermines even further the idea of a sharply discontinuous development of language over evolutionary time, and argues that we take a longer view of language evolution.

5. Future Research

It is almost surely the case that we have not fully mined the available clues for language evolution to date. As examples of intriguing future directions that language evolution research might proceed, three areas that may provide potentially groundbreaking data will be

highlighted. First, many new tools have been developed for mathematically describing complex morphological shapes, and these may allow us to extract additional clues from endocasts beyond what we have data for already. At present, we do not know fully what we can and cannot say about the brains and behaviors of individuals from their endocasts alone. There is clearly a degree of information loss, but we simply don't know how large it is. Using MRI and CT scanning technologies, it is possible to determine how closely different parts of the endocranial surface match the underlying brain of both humans and apes, and this will help clarify this issue. In addition, non-rigid deformation techniques, among others, can be applied to describe in detail species differences in endocranial surfaces (e.g., Schoenemann et al. 2011; Schoenemann et al. 2010). Correlations with behavioral differences can then be assessed at different locations on the endocasts, thereby allowing us to assess whether, for example, the size of Broca's cap predicts something about vocalizations, or other language relevant behaviors. This will then allow us to better understand what these endocranial features might be telling us.

Another intriguing area involves exploring the evolutionary precursors of language areas. Apes and monkeys appear to have homologs of language areas, such as Broca's and Wernicke's (Striedter 2005), but we do not currently fully understand how these areas function in these non-human species. An evolutionary perspective predicts that they process information in ways that—though not part of language *per se*—would be obviously useful for modern human language, perhaps with some minor modifications. One hypothesis that is currently being investigated is that Broca's area in both humans and other primates is involved in extracting and paying attention to sequential patterns of stimuli from the environment. This basic useful function would explain why it has been hijacked for language processing in humans. To explore this, non-linguistic tasks that activate Broca's area in humans (of which implicitly learning basic sequential patterns appears to be one Christiansen et al. 2002; Petersson et al. 2010) can be investigated in apes and other non-human primates, to see if they also activate their Broca's area homologs (Schoenemann 2010a). If this turns out to be the case, it would suggest that Broca's area evolved for a more general purpose, but one that would later be very useful for language. This would be a prime example of language (metaphorically) adapting to the human brain, rather than the reverse (e.g., Christiansen and Chater 2008).

Lastly, there is likely much more to be gained from computational approaches that attempt to model the evolution of language. This approach has yielded important insights into the process, showing that a great deal of linguistic structure is basically implicit in socially interactive communication itself, as emergent phenomenon (Gong et al. 2005; Gong et al. 2009; Ke et al. 2002; Kirby 2002; Kirby and Christiansen 2003; Steels 2011). These are surprising results to many theorists, particularly those not well versed in evolutionary theory, but they serve to highlight the pitfalls of relying too heavily on intuition when attempting to explain evolutionary processes. Professor Wang himself realized early on the importance and usefulness of computational studies for studying language evolution, and strongly encouraged their use among his students and colleagues. An application of these methods that might yield clues specifically to the time course of language evolution would be to explore the interplay between increasing conceptual complexity and increasing symbolic conventionalization over time. To the extent that such studies may show the former can drive the latter, we may be able to better anchor

the argument that increasing brain size—as a proxy for conceptual complexity— is likely telling us something about language evolution itself. Depending on how tight the linkage might turn out to be between conceptual complexity and symbolic conventionalization in such computational studies, one might be able to use computational data to make fairly good predictions about the development of language itself from the fossil record.

These by no means exhaust the possible future directions language evolution research can proceed, but they are a sample of some intriguing lines of inquiry. There is much work to be done in the area of language evolution.

6. Conclusions

Language is not a single, unitary behavioral capacity. As such, different components of it will likely have independent—though obviously connected—evolutionary histories. Applying evolutionary principles to language leads to the conclusion that it evolved through the modification of pre-existing cognitive abilities, and not from the evolution of wholly new ones. Several obvious pre-adaptations set the stage for language, including the inherently communicative type of interactive sociality practiced by primates generally, the existence of distinct mental concepts (though presumed to be not as rich as in modern humans), the ability to code these concepts with symbolic behavior, including rudimentary syntax.

Given this, dating the origin of language is problematic, since different components likely evolved at different times, and some cognitive circuits important for language predated the human lineage altogether. While none of the evidence is unequivocal, there are a great many clues pointing to a deeply ancient history for language origins. Evidence used to suggest a very late origin (i.e., either ~150,000 years ago at the appearance of anatomically modern *Homo sapiens*, or ~40,000 years ago at the dramatic increase in material culture that marks the beginning of the Upper Paleolithic) rely on highly questionable assumptions, e.g., that art or other aspects of behavior that is evident archaeologically could only be accomplished if people had language, or that the size of the vertebral column predicts language use, or that language requires a wide phonetic range and that we can reliably detect this in the fossil record. Attempts to estimate phonetic abilities of fossil hominins actually point to important changes dating back to early *Homo*, over ~1 million years ago. Genetic evidence of FOXP2 in Neanderthal ancient DNA also suggests language-relevant changes significantly predating *Homo sapiens*. Finally, a good argument can be made that brain size itself should be seen as a proxy for language evolution. Larger brains suggest both increased interactive—and hence communicative—sociality, as well as increased complexity and subtlety in conceptual thought. Both of these are fundamental to language, and arguably drove language evolution from its simplest beginnings to its current complexity.

The past 50 years have seen a number of creative attempts to extract new information relevant to language evolution out of the fragmentary fossil record. It is almost surely the case that more clues can be extracted, as we learn more and more about the relationships linking skull

to brain to behavior. The tools available today to study both morphology and behavior are much more powerful than in the past, and it is likely that much more will be learned about language evolution. Professor Wang's curiosity in language evolution, his extensive interdisciplinary interests and understanding, and his recognition of the fundamental importance of the question, have had a deep and lasting influence in the field. He remains an inspiration to his students.

REFERENCES

- Albanese, E., A. Merlo, A. Albanese, and E. Gomez. 1989. Anterior Speech Region: Asymmetry and Weight-Surface Correlation. *Archives of Neurology* 46 (3): 307–310.
- Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In *Evolutionary biology and human social behavior*, eds. N. A. Chagnon, and W. Irons, 402–433. North Scituate, Massachusetts: Duxbury Press.
- Arensburg, B., L. A. Schepartz, A. M. Tillier, B. Vandermeersch, and Y. Rak. 1990. A reappraisal of the anatomical basis for speech in Middle Palaeolithic hominids. *American Journal of Physical Anthropology* 83 (2):137–146.
- Barsalou, L. W. 2010. Grounded cognition: Past, present, and future. *Topics in Cognitive Science* 2 (4): 716–724.
- Bear, M. F., B. W. Connors, and M. A. Paradiso. 2007. *Neuroscience: Exploring the brain*. Baltimore, Philadelphia, PA: Lippincott Williams & Wilkins.
- Bergman, T. J., J. C. Beehner, D. L. Cheney, and R. M. Seyfarth. 2003. Hierarchical classification by rank and kinship in baboons. *Science* 302:1234–1236.
- Bickerton, D. 1995. *Language and human behavior*. Seattle: University of Washington Press.
- Broca, P. 1861. Remarques sur le siege de la faculte du langage articule, suivies d'une observation d'aphemie (perte de la parole). *Bulletins de la Societe anatomique* (Paris), 2e serie 6:330–357.
- Burr, D. B. 1976. Neandertal vocal tract reconstructions: A critical appraisal. *Journal of Human Evolution* 5:285–290.
- Byrne, R. W., and N. Corp. 2004. Neocortex size predicts deception rate in primates. *Proc Biol Sci* 271 (1549): 1693–1699.
- Cantalupo, C., and W. D. Hopkins. 2001. Asymmetric Broca's area in great apes. *Nature* 414 (6863): 505–505.

- Changizi, M. A., and S. Shimojo. 2005. Parcellation and area-area connectivity as a function of neocortex size. *Brain, Behavior and Evolution* 66 (2): 88–98.
- Cheney, D. L., and R. M. Seyfarth. 1990. *How monkeys see the world*. Chicago: University of Chicago Press.
- Chomsky, N. 1972. *Language and mind*. New York: Harcourt Brace Jovanovich, Inc.
- Christiansen, M. H. 1994. Infinite languages, finite minds: Connectionism, learning and linguistic structure [Unpublished PhD dissertation]. Edinburgh, Scotland: University of Edinburgh.
- Christiansen, M. H., and N. Chater. 2008. Language as shaped by the brain. *Behavioral and Brain Sciences* 31:489–509.
- Christiansen, M. H., R. A. Dale, M. R. Ellefson, and C. M. Conway. 2002. The role of sequential learning in language evolution: Computational and experimental studies. In *Simulating the evolution of language*, eds. A. Cangelosi and D. Parisi, 165–187. New York: Springer-Verlag Publishing.
- Clarke, E., U. H. Reichard, and K. Zuberbuhler. 2006. The syntax and meaning of wild gibbon songs. *PLoS ONE* 1:e73.
- Clegg, M., and L. C. Aiello. 2000. Paying the price of speech? An analysis of mortality statistics for choking on food. *American Journal of Physical Anthropology* S30:126.
- Croft, W. 2000. *Explaining language change: An evolutionary approach*. Harlow, Essex: Longman.
- Damasio, A. R., and Damasio, H. 1992. *Brain and language*. *Scientific American* 267 (3): 89–95.
- de Lumley, H. 1969. A Paleolithic Camp at Nice. *Scientific American* 220 (5): 42–50.
- Deacon, T. W. 1997. *The symbolic species: The co-evolution of language and the brain*. New York: W. W. Norton.
- DeGusta, D., W. H. Gilbert, and S. P. Turner. 1999. Hypoglossal canal size and hominid speech. *Proceedings of the National Academy of Sciences of the United States of America* 96 (4): 1800–1804.
- Denes, P. B., and E. N. Pinson. 1963. *The speech chain*. Garden City, New York: Anchor Press/Doubleday.
- Duchin, L. E. 1990. The evolution of articulate speech: Comparative anatomy of the oral cavity in Pan and Homo. *Journal of Human Evolution* 19:687–697.
- Dunbar, R. 1996. *Grooming, gossip and the evolution of language*. London: Faber and Faber.

- Dunbar, RIM. 2003. The social brain: Mind, language, and society in evolutionary perspective. *Annual Review of Anthropology* 32:163–181.
- Durham, W. H. 1991. *Coevolution: genes, culture, and human diversity*. Stanford, Calif.: Stanford University Press.
- Enard, W., M. Przeworski, S. E. Fisher, C. S. Lai, V. Wiebe, T. Kitano, A. P. Monaco, and S. Paabo. 2002. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* 418 (6900): 869–872.
- Evans, N., and S. C. Levinson. 2009. The myth of language universals: Language diversity and its importance for cognitive science. *Behavioral and Brain Sciences* 32 (05): 429–448.
- Falk, D. 1975. Comparative anatomy of the larynx in man and chimpanzee: Implications for language in Neandertal. *American Journal of Physical Anthropology* 43:123–132.
- . 1983. Cerebral cortices of East african early hominids. *Science* 221 (4615): 1072–1074.
- Falzi, G., P. Perrone, and L. A. Vignolo. 1982. Right-Left Asymmetry in Anterior Speech Region. *Archives of Neurology* 39 (4): 239–240.
- Fetzer, J. H. 1988. Signs and minds: An introduction to the theory of semiotic systems. In *Aspects of artificial intelligence*, ed. J. H. Fetzer, 133–161. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Fitch, W. T., and D. Reby. 2001. The descended larynx is not uniquely human. *Proceedings of the Royal Society of London Series B: Biological Sciences* 268 (1477): 1669–1675.
- Foundas, A. L., C. M. Leonard, R. L. Gilmore, E. B. Fennell, and K. M. Heilman. 1996. Pars triangularis asymmetry and language dominance. *Proceedings of the National Academy of Sciences of the United States of America* 93 (2): 719–722.
- Friedman, M. J., and W. Trager. 1981. The biochemistry of resistance to malaria. *Scientific American* 244 (3): 154–164.
- Gardner, R. A., and B. T. Gardner. 1984. A vocabulary test for chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology* 98:381–404.
- Gong, T., J. W. Minett, J. Ke, J. H. Holland, and W. S. Y. Wang. 2005. Coevolution of lexicon and syntax from a simulation perspective. *Complexity* 10 (6): 50–62.
- Gong, T., J. W. Minett, and W. S. Y. Wang. 2009. A simulation study exploring the role of cultural transmission in language evolution. *Connection Science* 22 (1): 69–85.
- Gopnik, M., and Crago, M. B. 1991. Familial aggregation of a developmental language disorder. *Cognition* 39 (1): 1–50.

- Haiman, J. 1985. *Natural Syntax: Iconicity and erosion*. Cambridge: Cambridge University Press.
- Hauser, M. D., N. Chomsky, and W. T. Fitch. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1569–1579.
- Henshilwood, C. S., F. d'Errico, K. L. van Niekerk, Y. Coquinot, Z. Jacobs, S-E. Lauritzen, M. Menu, and R. García-Moreno. 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science* 334 (6053): 219–222.
- Henshilwood, C. S., and C. W. Marean. 2003. The origin of modern human behavior: Critique of the models and their test implications. *Current Anthropology* 44 (5): 627–651.
- Holloway, R. L., Broadfield, D. C., and M. S. Yuan. 2004. *The human fossil record, Volume 3. Brain endocasts—The paleoneurological evidence*. Hoboken: John Wiley & Sons.
- Hunt, K. D. 1994. The evolution of human bipedality: Ecology and functional morphology. *Journal of Human Evolution* 26 (3): 183–202.
- Hurst, D. 2011. Acoustic communities: An amendment to the social brain hypothesis. *American Journal of Physical Anthropology* 144 (Supplement 52): 172.
- Isaac, G. L. 1976. Stages of cultural elaboration in the pleistocene: Possible archaeological indicators of the development of language capabilities. *Annals of the New York Academy of Sciences* 280 (1): 275–288.
- Jackendoff, R. 2002. *Foundations of language: Brain, meaning, grammar, evolution*. New York: Oxford University Press.
- Kay, R. F., Cartmill, M., and Balow, M. 1998. The hypoglossal canal and the origin of human vocal behavior. *Proceedings of the National Academy of Sciences USA* 95:5417–5419.
- Ke, J., and Holland, J. H. 2006. Language origin from an emergentist perspective. *Applied Linguistics* 27 (4): 691–716.
- Ke, J., J. Minett, C-P. Au, and W. S. Y. Wang. 2002. Self-organization and selection in the emergence of vocabulary. *Complexity* 7 (3): 41–54.
- Kirby, S. 2002. Natural language from artificial life. *Artificial Life* 8 (2): 185–215.
- Kirby, S., and M. H. Christiansen. 2003. From language learning to language evolution. In *Language evolution*, eds. M. H. Christiansen and S. Kirby, 272–294. Oxford: Oxford University Press.
- Klein, R. G., and B. Edgar. 2002. *The dawn of human culture*. New York: John Wiley & Sons.

- Krause, J., C. Lalueza-Fox, L. Orlando, W. Enard, R. E. Green, H. A. Burbano, J. J. Hublin, C. Hanni, J. Fortea, M. de la Rasilla et al. 2007. The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology* 17 (21): 1908–1912.
- Laitman, J. T. 1983. The evolution of the hominid upper respiratory system and implications for the origins of speech. In *Glossogenetics: The Origin and Evolution of Language*, *Proceedings of the International Transdisciplinary Symposium on Glossogenetics*, ed. E. de Grolier, 63–90. Paris: Harwood Academic Publishers.
- . 1985. Evolution of the hominid upper respiratory tract: The fossil evidence. In *Hominid evolution: Past, present and future*, eds. P. V. Tobias, V. Strong, and H. White, 281–286. New York: Alan R. Liss.
- Laitman, J. T., and R. C. Heimbuch. 1982. The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. *American Journal of Physical Anthropology* 59:323–344.
- Laitman, J. T., R. C. Heimbuch, and E. S. Crelin. 1979. The basicranium of fossil hominids as an indicator of their upper respiratory systems. *American Journal of Physical Anthropology* 51:15–34.
- Langacker, R.W. 1987. *Foundations of cognitive grammar*. Stanford: Stanford University Press.
- Latimer, B., and Ohman, J. C. 2001. Axial dysplasia in *Homo erectus*. *Journal of Human Evolution* 40 (3): A12.
- Lieberman, P. 1984. *The biology and evolution of language*. Cambridge, Massachusetts: Harvard University Press.
- Livingstone, F. B. 1958. Anthropological implications of sickle cell gene distribution in West Africa. *American Anthropologist* 60:533–562.
- Mayr, E. 1978. Evolution. *Scientific American* 239:47–55.
- Meyer, M. R. 2003. Vertebrae and language ability in early hominids. Annual Meeting of the Paleo Anthropology Society. Tempe, Arizona.
- . 2005. Functional biology of the *Homo erectus* axial skeleton from Dmanisi, Georgia [Dissertation]. Philadelphia: University of Pennsylvania.
- O’Grady, W. 1987. *Principles of grammar and learning*. Chicago: University of Chicago Press.
- Oakley, K. P. 1973. Fossils collected by the earlier palaeolithic men. *Mélanges de préhistoire, d’archéocivilization et d’ethnologie offerts à André Varagnac*, 581–584. Paris: Serpen.
- . 1981. Emergence of higher thought 3.0-0.2 Ma B. P. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 292 (1057): 205–211.

- Peirce, C. S. 1867. On a new list of categories. *Proceedings of the American Academy of Arts and Sciences* 7:287–298.
- Petersson, K. M., V. Folia, and P. Hagoort. 2010. What artificial grammar learning reveals about the neurobiology of syntax. *Brain and Language*.
- Pinker, S. 1994. *The language instinct: How the mind creates language*. New York: Harper Collins Publishers, Inc.
- Pinker, S., and P. Bloom. 1990. Natural language and natural selection. *Behavioral and Brain Sciences* 13 (4): 707–784.
- Posner, M. I., and M. E. Raichle. 1994. *Images of mind*. New York: W. H. Freeman.
- Premack, A. J., and D. Premack. 1972. Teaching language to an ape. *Scientific American* 227 (October): 92–99.
- Ringo, J. L. 1991. Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution* 38:1–6.
- Savage-Rumbaugh, E. S., J. Murphy, R. A. Sevcik, K. E. Brakke, S. L. Williams, and D. M. Rumbaugh 1993. Language comprehension in ape and child. *Monographs of the Society for Research in Child Development* 58 (3–4): 1–222.
- Savage-Rumbaugh, E. S., and D. M. Rumbaugh. 1993. The emergence of language. In *Tools, language and cognition in human evolution*, eds., K. R. Gibson, and T. Ingold, 86–108. . Cambridge: Cambridge University Press.
- Savage-Rumbaugh, S., D. Rumbaugh, and W. M. Fields. 2009. Empirical kanzi: The ape language controversy revisited. *Skeptic* 15 (1): 25–33.
- Sawaguchi, T. 1988. Correlations of cerebral indices for ‘extra’ cortical parts and ecological variables in primates. *Brain Behavior and Evolution* 32 (1988): 129–140.
- . 1990. Relative brain size, stratification, and social structure in Anthropoids. *Primates* 31 (2): 257–272.
- Sawaguchi T., and H. Kudo. 1990. Neocortical development and social structure in primates. *Primates* 31 (2): 283–289.
- Schick, K. D., and N. Toth. 1993. *Making silent stones speak: Human evolution and the dawn of technology*. Touchstone.
- Schmandt-Besserat D. 1991. The earliest precursor of writing. In *The emergence of language: development and evolution : readings from scientific american magazine*, ed. W. S. Y. Wang. W. H. Freeman.

- Schoenemann, P. T. 1999. Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines* 9:309–346.
- . 2005. Conceptual complexity and the brain: Understanding language origins. In *Language Acquisition, Change and Emergence: Essays in Evolutionary Linguistics*, eds. W. S-Y. Wang and J. W. Minnett, 47–94. Hong Kong: City University of Hong Kong Press.
- . 2009a. Brain Evolution Relevant to Language. In *Language, evolution, and the brain*, ed. J. Minnett, and W. S-Y. Wang. Hong Kong: City University of Hong Kong Press.
- . 2009b. *Evolution of brain and language*. *Language Learning* 59 (s1): 162–186.
- . 2010a. The importance of exploring non-linguistic functions of human brain language areas for explaining language evolution. In *The Evolution of Language; Proceedings of the 8th International Conference (EVO LANG8)*, eds. A. D. M. Smith, M. Schouwstra, B. de Boer, and K. Smith, 485–486. London: World Scientific Publishing.
- . 2010b. The meaning of brain size: The evolution of conceptual complexity. *Human brain evolving: Papers in honor of Ralph Holloway*. Bloomington, Indiana: Stone Age Institute Press.
- . in press. Brain evolution. In *A companion to paleoanthropology*, ed. D. R. Begun. Blackwell.
- Schoenemann, P. T., T. F. Budinger, V. M. Sarich, and W. S. Wang. 2000. Brain size does not predict general cognitive ability within families. *Proceedings of the National Academy of Sciences of the United States of America* 97 (9): 4932–4937.
- Schoenemann, P. T., R. Holloway, J. Monge, B. Avants, and J. Gee. 2011. Differences in endocranial shape between Homo and Pongids assessed through non-rigid deformation analysis of high-resolution CT images. *American Journal of Physical Anthropology* 144 (Supplement 52): 265–266.
- Schoenemann, P. T., R. L. Holloway, B. B. Avants, and J. C. Gee. 2008. Endocast asymmetry in pongids assessed via non-rigid deformation analysis of high-resolution CT images. *American Journal of Physical Anthropology* 135 (Supplement 46): 187–188.
- Schoenemann, P. T., J. Monge, B. B. Avants, and J. C. Gee. 2010. Creating statistical atlases of modern primate endocranial morphology using non-rigid deformation analysis of high-resolution CT images. *American Journal of Physical Anthropology* 141 (Supplement 50): 208–209.
- Schoenemann, P. T., and W. S.-Y. Wang. 1996. Evolutionary principles and the emergence of syntax. *Behavioral and Brain Sciences* 19 (4): 646–647.
- Seyfarth, R. M., and D. L. Cheney. 2003. Meaning and Emotion in Animal Vocalizations. *Annals of the New York Academy of Sciences* 1000 (1): 32–55.

- Shen, Z-W. 1997. Exploring the dynamics aspect of sound change. *Journal of Chinese Linguistics Monograph* 11.
- Steels, L. 2011. Modeling the cultural evolution of language. *Phys Life Rev* 8 (4): 339–356.
- Striedter, G. F. 2005. *Principles of brain evolution*. Sunderland, MA: Sinauer Associates.
- Tattersall, I. 1998. *Becoming human: Evolution and human uniqueness*. New York: Harcourt Brace.
- Tobias, P. V., and B. Campbell. 1981. The Emergence of Man in Africa and Beyond [and Discussion]. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 292(1057): 43–56.
- Vargha-Khadem, F., K. Watkins, K. Alcock, P. Fletcher, and R. Passingham. 1995. Praxic and nonverbal cognitive deficits in a large family with a genetically transmitted speech and language disorder. *Proceedings of the National Academy of Sciences of the United States of America* 92 (3): 930–933.
- Walker, A., and Shipman, P. 1996. *The wisdom of the bones: In search of human origins*. New York: Knopf.
- Wang, W. S.-Y. 1991. Explorations in language evolution. *Explorations in language*, 105–131. Taipei, Taiwan: Pyramid Press.
- Wang, W. S.-Y., J. Ke, and J. W. Minett. 2004. Computational studies of language evolution. In *Computational linguistics and beyond*, eds. C. R. Huang, and W. Lenders, 65–106. Academica Sinica: Institute of Linguistics.
- Zuberbuhler, K. 2000. Interspecies Semantic Communication in Two Forest Primates. *Proceedings: Biological Sciences* 267 (1444): 713–718.
- Zuberbuhler, K. 2002. A syntactic rule in forest monkey communication. *Animal Behaviour* 63:293–299.