

3

Conceptual Complexity and the Brain: Understanding Language Origins

P. Thomas Schoenemann
University of Pennsylvania

Abstract

The evolutionary process works by modifying pre-existing mechanisms, which makes continuity likely. A review of the evidence available to date suggests that there are many aspects of language that show evolutionary continuity, though the direct evidence for syntax and grammar is less clear. However, the universal features of grammar in modern human languages appear to be essentially descriptions of aspects of our basic conceptual universe. It is argued that the most parsimonious model of language evolution involves an increase in conceptual/semantic complexity, which in turn drove the acquisition of syntax and grammar. In this model, universal features of grammar are actually simply reflections of our internal conceptual universe, which are manifested culturally in a variety of ways that are consistent with our pre-linguistic cognitive abilities. This explains both why grammatical rules vary so much across languages, as well as the fact that the commonalities appear to be inherently semantic in nature. An understanding of the

way in which concepts are instantiated in the brain, combined with a comparative perspective on brain structure/function relationships, suggest a tight relationship between increasing brain size during hominid evolution and increasing conceptual complexity. A simulation using populations of interacting artificial neural-net agents illustrating this hypothesis is described. The association of brain size and conceptual complexity suggests that language has a deep ancestry.

1. Introduction

Since language is one of the defining characteristics of the human condition, the riddle of its origin and evolution is one of the most intriguing and fundamental questions in all of evolutionary biology. As with all evolutionary reconstructions, we are limited in the data available on which to build our explanatory models. But the problem of unraveling language evolution is of course made even harder by the fact that speech acts themselves are inherently ephemeral, and the fossil and archaeological clues relevant to language are only tantalizingly equivocal (Wang, 1991b). Language behavior, in short, does not fossilize (Hauser et al., 2002). Thus, we are even further removed from the direct behavior of interest than for other important hominid adaptive behaviors such as bipedalism or the use of fire. It is exactly for this reason that a believable explanation will rely even more critically on a clear understanding of exactly how the evolutionary process works. Not all scenarios are equally likely from an evolutionary perspective. We must of course understand the complexity of natural language in humans, and place it within the proper comparative, cross-species context. But a believable characterization of natural language itself will — whether we like it or not — necessarily be constrained by what is evolutionarily likely. A model of language which is evolutionarily implausible is not just “. . . a problem for the biologist . . . ” (Chomsky, 1972: 70), but actually calls the model itself into question. A consideration of the problem in this light shows that the

key to the puzzle is *not* the evolution of language-specific brain modules devoted solely for syntax. Instead, it is argued language evolved through the modification and elaboration of pre-existing cognitive mechanisms, with non-genetic cultural evolutionary processes playing a key role.

2. How Evolution Works

The evolutionary process operating on biology creates and maintains complexity by capitalizing on random changes that are introduced into a population. While these changes can have large or small effects, the ones that happen to have small incremental effects also happen to be more likely to be retained. This is because the likelihood that a large mutation will have a positive effect on the fitness of an individual will *decrease* with the size of the change. Each of these intermediate incremental steps along an evolutionary pathway to some adaptation must be beneficial (ultimately with respect to reproduction). As Jacob (1977) notes, this means that “Evolution does not produce novelties from scratch. It works on what already exists, either transforming a system to give it new functions or combining several systems to produce a more elaborate one,” (p. 1164). This further implies that homologies will be the rule, rather than the exception (Schoenemann, 1999). That is, we should specifically be looking for them.

It is also important to recognize that in an important sense, behavioral evolution drives biological evolution. Mayr (1978) points out that “there is little doubt that some of the most important events in the history of life, such as the conquest of land or of the air, were initiated by shifts in behavior.” (p. 55, quoted in Lieberman, 1984). It is true that the biology must already have been such that particular behavioral changes would be possible when the time came, but the appropriate behavioral flexibility necessarily existed prior to — and for reasons other than — the adaptive need of the organism to shift its behavior in any particular direction. The complete suite of biological changes that made terrestrial living

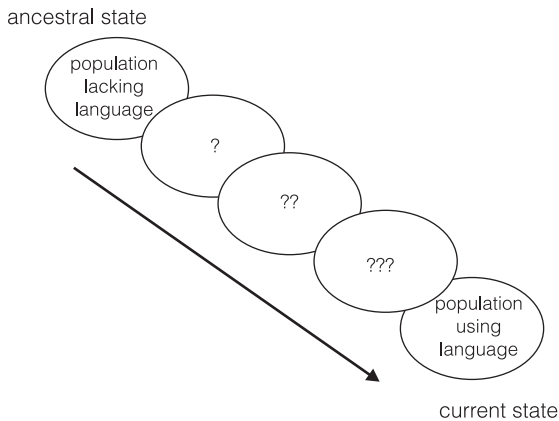
adaptive did not all occur prior to the emergence of the first land vertebrates. They occurred only as the organisms pushed the limits of their behavioral flexibility specifically in the direction of increasingly terrestrial living.

In order to properly conceptualize the evolution of language, it is necessary to keep clearly in mind the two endpoints (Figure 1). In the beginning there existed a population of hominids lacking language, while at the end there exists a population *with* language. In order for this change to have occurred, it must necessarily have been true that there was some adaptive benefit of some kind to linguistic behavior (broadly defined). It does not matter for the present argument whether this benefit was related to communication or to some aspect of cognition or thinking, but some benefit must have accrued to individuals with better language abilities, or else we would not now be using language. Furthermore, this would have to have been true *within* each intermediate population, on average. Given this, it follows that if an individual within any one of these populations were able to use some pre-existing cognitive abilities to better accomplish some linguistically relevant processing, this individual would gain immediate advantages by doing so. Behavioral adaptations that require minimal genetic changes will be favored at each step. Given that this was always the case, the whole evolutionary process would necessarily have been biased towards incremental changes in pre-existing mechanisms, and decidedly *not* towards the evolution of completely new, language-specific cognitive modules.

In general, the evolutionary process does not favor the evolution of domain-specific cognitive modules, particularly if any way can be found to accomplish the task by modifying pre-existing mechanisms. This is true in spite of the argument made by some evolutionary psychologists that domain-general mechanisms would necessarily be inferior to dedicated, domain-specific mechanisms, and hence will be inherently unlikely. The flaw in this argument is that it does not properly acknowledge the process of evolutionary change. Regardless of how much better a particular domain-specific mechanism might ultimately be if it could be perfectly engineered for

its assigned task, the evolutionary process itself is inevitably biased towards modifying mechanisms that are (by definition) more domain general. As a corollary to this, it is clear that meaningfully important continuities with other species are to be expected (Schoenemann, 1999). In fact, continuities are so ubiquitous in biology that the burden of proof must lie with models that deny continuities out of hand. Specifically with respect to language, there is in fact a great deal of evidence for continuity in the mechanisms involved in sound production and perception, those underlying semantics, and possibly even for syntax.

Figure 1
The evolutionary transition to language



The transition to language involved a series of populations, starting from one that lacked language and ending at one that had acquired fully modern language. Each intermediate population would have been incrementally closer to the modern condition, on average, compared to the one before it. Any behavioral changes that could have accomplished these incremental steps with pre-existing cognitive abilities and anatomical features would necessarily have been favored, thereby biasing the evolution of language toward the modification of existing abilities, and away from the creation of wholly new structures and abilities.

3. Evidence for Continuity

3.1 Continuity in sound production

Continuity is evident with respect to sound production in features of the structure of the larynx, the use of particular features of the speech signal to convey meaning, and the musculature and neurological control used to create distinctive acoustic features. The larynx is responsible for producing the initial vibration that forms the foundation for speech. It turns out that our larynx is not fundamentally different from that of other mammals (Negus, 1949), and furthermore, animals which use their forelimbs for climbing generally have well developed larynges (Denes and Pinson, 1963). This is because the larynx functions not only to keep food from getting into the lungs, but also to seal air into the lungs under pressure, thereby strengthening the thorax considerably and allowing more effective use of the forelimbs. Humans are most closely related to the modern apes, with whom we share an upper body anatomy adapted to brachiation (a mode of locomotion characterized by swinging underneath tree branches with the forearms) which means that pre-linguistic hominids inherited a well developed larynx from their proto-ape ancestors.

The vibration imparted by the larynx is then filtered through the supralaryngeal vocal tract, emphasizing some frequency bands (which are called ‘formants’) and deemphasizing others. The use of formants to convey information is not unique to human language, however. An excellent example occurs in the mating calls of bullfrogs from the species *Rana catesbeiana* (Capranica, 1965; Lieberman, 1984). These bullfrogs will join in a chorus with a synthesized version of their mating call only if it has concentrations of acoustic energy at either the first or second formants, or both (Capranica, 1965).

It is also true that different animals, including humans, use similar sound characteristics to communicate the same kinds of underlying meanings. Other animals use pitch to indicate relative submissiveness (high frequency bias) vs. dominance/aggressiveness (low frequency bias), and this bias is also found cross-linguistically

in humans (Kingston, 1991; Ohala, 1983).

In order to produce the complex sound sequences of language, humans have evolved remarkable neural control over the muscles of the face, larynx, pharynx, tongue, mandible, diaphragm, and ribs. These muscles are innervated by motor portions of several cranial nerves: 1) the mandibular division of the trigeminal (Vth) which controls the muscles of mastication (i.e. the movement of the lower jaw), 2) the facial (VIIth) which controls the muscles of facial expression, 3) the glossopharyngeal (IXth) which controls the stylopharyngeus muscle (and may also innervate portions of the superior pharyngeal constrictor muscle), 4) the vagus (Xth) which controls the levator veli palatini, middle and inferior pharyngeal constrictors, salpingopharyngeus, and all the laryngeal muscles, and 5) the hypoglossal (XIIth) which controls the muscles of the tongue (Carpenter and Sutin, 1983). These motor fibers arise from various motor nuclei in the brainstem and constitute what may be considered the most basic level of speech control. The motor nuclei are in turn connected to various other neuroanatomical regions. The motor nuclei for muscles of the face, jaw, and tongue receive direct projections from the various motor regions of the cerebral cortex, as well as indirect connections (via the reticular formation and central gray regions of the brainstem) with the prefrontal cortex, cingulate cortex (considered part of the limbic system), and diencephalon (Deacon, 1989). The laryngeal musculature also appears to receive direct innervation from the motor cortex as well as indirect innervation (again, via the reticular formation and central gray regions of the brainstem) from the cingulate cortex and the diencephalon (Deacon, 1989; Jürgens and Zwirner, 2000).

It is important to understand that this complexity is not unique to humans, however. The basic patterns of neural connections controlling the musculature involved in vocalization are the same in other primates (and mammals generally). The differences that have been documented so far occur only in the relative proportions and emphases of the different connections (Deacon, 1989). The basic rudiments of human neural connections are thought to be extremely old.

It is also known that the basic cortical connections relevant to language processing (as inferred from human clinical and electrical stimulation studies) match connections found in axonal tracer studies of monkey cortical connections (Deacon, 1988; Deacon, 1989; Galaburda and Pandya, 1982; Jürgens and Zvirner, 2000). For example, Broca's and Wernicke's areas (usually defined as including the posterior inferior frontal convexity and posterior third portion of the superior temporal gyrus, respectively), which were the first two areas found to be critical for language processing, are connected by a major tract known as the arcuate fasciculus. Since both these areas mediate different aspects of language, they must need to communicate in some way in order for language processing to proceed normally. An obvious place to look for human/non-human differences would be in the connection between these two areas. However, Deacon (1984) has shown that the Broca's and Wernicke's homologs in macaques share the same direct connections that are seen in humans. Deacon (1988) notes that ". . . all of the major pathways presumed to link language areas in humans are predicted by monkey tracer data," (p. 368). It would appear that monkeys (which have been separate from the lineage leading to humans for ~25 million years, Sarich and Cronin, 1976) have the same basic set of neural connections even though they do not have similar behavioral abilities. What clearly has happened is a modification of existing architecture, not a major reorganization.

3.2 Continuity in perception

While it is generally assumed that speech perception in humans has required some sort of neuroanatomical evolutionary change, there is nevertheless unmistakable evidence of continuity here as well. This can be seen not only in the perception of formants, but also in many of the sounds that characterize language. In order to differentiate vowels, it is necessary to be able to perceive rapid changes in formant frequencies. It turns out that the structures in the cochlea of the inner ear responsible for translating air pressure fluctuations

(i.e., sound) into nerve impulses are almost ideally constructed to operate as a sound spectrogram analyzer (Denes and Pinson, 1963). Formants are thus exactly the kind of information that one would expect to be particularly salient. However, our auditory system did not appear in hominids for the express purpose of allowing the development of language. It is essentially the same as is found in all mammals, and thus likely dates back at least 200 million years (Lieberman, 1984).

A number of studies of non-human animals provide behavioral evidence of the ability to extract the patterns of formant frequencies embedded in sound waves. For example, it has been shown that mynah birds “copy” human speech by mimicking the relative changes in formant frequencies (they produce two different tones at a time, one from each syrinx, Klatt and Stefanski, 1974; Lieberman, 1984). Obviously, if they can copy patterns of formant frequencies in some fashion, they must be able to perceive them. Fouts et al. (1976) have shown that common chimpanzees (*Pan troglodytes*) can understand spoken English. Savage-Rumbaugh et al. (1993) reports that the pygmy chimpanzee (*Pan paniscus*) Kanzi correctly identifies a large array of spoken English words (even in strict double-blind experiments), and is also able to do this with computer-synthesized versions of the words. Although Kanzi might simply be doing some gestalt pattern-matching, his ability to perform these kinds of tasks suggests that pygmy chimps can hear at least some of the same kinds of phonemic distinctions that humans use, and thus has the auditory apparatus to distinguish the essential components of the rapid formant transitions (and other key acoustic features of speech).

There are suggestions that the human acoustic perceptual abilities are fine-tuned to the specific features of speech. For example, it appears that humans are better able to follow streams of phonemes than series of non-phonemic sounds, and phonemes can be decoded by listeners even though they vary tremendously in acoustic characteristics from speaker to speaker (particularly in the specific frequencies of the formants, Lieberman, 1984; 1988). However, given the abilities of language-trained chimps such as Kanzi, it is not clear whether the human abilities in this regard are

unique features specifically evolved in humans for language (again, Kanzi might simply be doing some gestalt pattern-matching), or simply extensions of abilities found in other animals.

Another possible example of continuity involves 'categorical perception', which occurs when auditory discrimination is greater at some points along an acoustic continuum than at others. These areas of greater discrimination often occur at phonemic boundaries, thereby facilitating speech perception (Liberman et al., 1957). This has been suggested for a number of features, including voice-onset-time (Kuhl, 1986; Kuhl and Miller, 1975), differences in the second formant transition (Mattingly et al., 1971), and even differences in the third formant transition, which is the acoustic basis for the distinction between /ra/ and /la/ in English (Miyawaki et al., 1975). The categorical nature of the perception of phonemes is fundamentally different from the perception of other dimensions of auditory stimuli, such as basic duration, frequency, and intensity of tones, which have been shown to be perceived in an essentially continuous fashion (Divenyi and Sachs, 1978; Kuhl, 1986; Snowdon, 1990). Although categorical perception was initially thought to indicate that humans had evolved unique neurological adaptations for decoding the speech signal (Kuhl, 1986), experiments reported on a range of animals have suggested non-linear discrimination functions similar to humans for at least some phonemic contrasts (Kluender et al., 1987; Kuhl and Padden, 1982; Kuhl and Padden, 1983; Kuhl and Miller, 1975; Kuhl and Miller, 1978; Morse and Snowden, 1975). However, many of these studies are methodologically suspect, for example training animals only on the end points of the continuum before testing intermediates (e.g., Kuhl and Miller, 1975; Kuhl and Miller, 1978). What is needed is to show that discrimination is greater in some parts of the continuum of interest without unintentionally inducing the animal to respond in this way as an artifact of the training method. At least some studies appear to have done this. Kuhl and Padden (1982) trained 3 macaques to indicate when they heard a change in stimuli (i.e., /a/ vs. /i/, the same vowel differing in pitch contour rise, and later syllable pairs differing only in initial consonants such as /va/ vs.

/sa/). The monkeys were then tested on how well they could detect pairs of computer-generated tokens along the /ba-pa/, /da-ta/, and /ga-ka/ continua, which all involve changes in voice-onset-time (VOT). Three pairs in each continua were tested, with each pair differing by exactly 20 ms in VOT. The pairs were equally spaced along the VOT continua, but only one pair straddled the human phonemic boundary. The monkeys were significantly more likely to indicate they heard a difference if the pairs straddled the human phonemic boundaries. Thus, at least some studies suggest a continuity with respect to categorical perception.

Regardless of the status of these studies, it is important to point out that the general prediction of evolutionary continuity is particularly clear for speech perception. During the earliest stages of evolution of language, sounds would have been adopted both for their ability to be clearly distinguished by existing perceptual systems, as well as for ease in being produced by the existing vocal apparatus. Selection would have operated on both of these systems simultaneously (Kuhl, 1986), and changes may well have occurred in both over the evolution of language, but the system would necessarily have been biased towards those features that were already salient to an ape perceptual auditory system.

3.3 Continuity in semantics

Complex organisms are able to make a larger number of distinctions in the varieties of perceptual information available to them than less complex organisms. These perceptual distinctions form the basis for conceptual categories. Bickerton (1990) argues that “The sea anemone . . . divides the world into ‘prey’ and ‘nonprey’, then divides the latter category into ‘potential predators’ and ‘others’, while the frog divides the world into ‘frogs’, ‘flying bugs’, ‘ponds’, and perhaps a few other categories like ‘large looming object (potential threat)’,” (p. 87). The kinds of categories that can be formed by complex organisms are not limited to specific sets of objects, like ‘flying bugs’ or ‘ponds’, of course. If they have multiple

senses interconnected to each other they can form more abstract categories such as 'running', 'sleeping', or 'friendship'.

It is true that the concepts recognized by one species may not be recognized by another. Dogs, for example, comprise one of many species that cannot differentiate as many colors as humans (Miller and Murphy, 1995; Neitz et al., 1989). Humans cannot hear the acoustic echoes that bats use to differentiate between an insect and a tree branch. Each species has evolved to pay attention to (i.e., form categories of) those parts of the environment that became most important for its own survival. Nevertheless, there is a substantial degree of overlap across species. Pigeons have been shown to have visual categories for such things as 'people', 'trees', 'fish', and even 'Snoopy cartoons' that are essentially the same as our own (Herrnstein, 1979). This clearly shows that, to a significant extent, human languages and cultures have made use of categories that are 'real' to a wide variety of animals.

Furthermore, it is clear that other animals can use arbitrary symbols to communicate aspects of their conceptual worlds. A number of studies have demonstrated the ability of non-human species to use vocal calls to mark aspects of their internal motivation. For example, in several species more calls are given when a greater quantity or quality of food is found (Dittus, 1984; Hauser and Wrangham, 1987; Marler et al., 1986a; Marler et al., 1986b; Snowdon, 1990). These examples represent indexical (as opposed to truly symbolic) signs in Peirce's semiotic framework (Agha, 1997), but they nevertheless indicate that an internal state can be marked with an external sign. These animals are not transmitting the emotion itself, they are transmitting a vocal sign of their emotional state.

More impressively, Seyfarth et al. (1980) showed that vervet monkeys use three different alarm calls that are specific to three different types of predator: eagles, snakes, and leopards. The lack of transfer of habituation between calls for different predators (Cheney and Seyfarth, 1988) suggests that the signals really do carry semantic meaning. Subsequent work has shown that the vervet monkey case is not unique: several species of monkeys have been

shown to use specific predator alarm calls in essentially the same manner (Zuberbuhler, 2000a; Zuberbuhler, 2000b; Zuberbuhler, 2001).

A number of studies clearly show that chimpanzees not only have semantic concepts, but also that they can assign and use arbitrary symbols to communicate information about them. Gardner and Gardner (1984) showed in double-blind tests that chimpanzees could correctly name (using sign language) objects that the experimenter/observer themselves could not see (thereby ruling out some form of ‘Clever Hans’ subtle cuing). Premack and Premack (1972) demonstrated that chimpanzees (*Pan troglodytes*) could use arbitrary symbols to communicate information about the concepts they represented. Asked to provide the color and shape of apples, for example, the chimp Sarah correctly chose the symbols for “red” and “circle”, even though her icon for apple (which was used to ask her the questions) was a blue triangle. Subsequent work by Savage-Rumbaugh and colleagues (1986) showed that chimps could be trained to use arbitrary symbols to ask for specific items from an array, to ask for items which were out of sight, to respond to symbols requesting items from another room, and ultimately to request another chimp to get items for them. The fact that chimps have been trained to communicate in these ways is evidence that they are able to 1) form mental concepts, 2) assign arbitrary symbols to these concepts, and 3) communicate specific ideas concerning these concepts via purely symbolic means. Their abilities are not identical to those of humans, it is true, but the differences are ones of degree, not of kind. The gap between what they demonstrate when reared as human children vs. in the wild as chimpanzees is not good evidence for discontinuity, moreover. The studies of captive animals show what is cognitively possible for an ape, given a humanlike learning environment.

3.4 Continuity in syntax and grammar

Of all aspects of language, syntax and grammar are the most difficult to demonstrate in non-human animals. Impressive abilities

have been shown for dolphins and sea lions (Schusterman and Gisinger, 1988), but these animals are quite distant from the human lineage, and therefore do not represent likely examples of evolutionary continuity. Zuberbuhler (2002) reports that Diana monkeys (*Cercopithecus diana*) behave differently to the alarm call of another primate, the Campbell's monkey (*Cercopithecus campbelli*), if the call is first preceded by another kind of distinctive 'boom' call. This would appear to be a very primitive type of syntactic rule: one type of call appears to modify the meaning of another call.

Premack and Premack (1972) showed that the chimp Sarah could mark argument relationships with an arbitrary device (in this case, serial order). While it is true that not all human languages require the use of serial order for this purpose, Sarah demonstrated that chimps have the cognitive structures that underlie the concept of "argument relationship" and furthermore, can use an arbitrary device to distinguish it. To argue that this is not evidence for continuity on the basis that human grammatical structures use many other devices in addition to serial order, is to misunderstand how evolution works.

Perhaps the best evidence of continuity comes again from Kanzi, who has demonstrated in a number of tests that he can respond appropriately to verbal commands, even ones that he had never been exposed to before (e.g., "Pour the lemonade in the Coke."). He responded correctly on 74% of 416 sentences in which the person giving the commands was not visible to Kanzi, and the person with him either covered their eyes (for the first 100 blind trials) or wore headphones playing loud music (for the remaining 316 blind trials) to ensure that they would not inadvertently cue him (Savage-Rumbaugh et al., 1993). At a minimum, Kanzi must have at least an incipient understanding that the relationship between sequences of symbols *itself* conveys meaning.

These abilities are quite limited with respect to humans, although the seeds of possibility are quite clearly apparent. Given the degree of continuity in various other aspects of language, and specifically how existing structures have been modified for use in

language, the null hypothesis should be that syntax and grammar can be explained in this way as well. To what extent is natural language grammar and syntax fundamentally different from other types of cognition? What exactly does natural language grammar look like and how should it be properly characterized?

4. Syntax and Grammar in Natural Languages

4.1 Characterizing Universal Grammar

Cross-linguistic studies of grammar and syntax make it evident that a tremendous amount of variation exists across languages (Croft, 2003). Furthermore, grammatical structures are known to change over relatively short periods of time (e.g., Ogura, 1993; Traugott, 1972). In addition, there are differing views on how to characterize grammar in the first place. Some linguists reject the view that formal mathematical structures are the appropriate model to describe grammar and heavily emphasize the semantic basis of language (Lakoff, 1987; Langacker, 1987; O’Grady, 1987). Some models of language origins do not see the question of grammar as central at all (e.g, Urban, 2002). Formal linguistic models have in fact not even been able to characterize English — one of the most intensively studied languages — in a completely satisfactory manner (Croft, 1991; Jackendoff, 1994; Lieberman, 2002). Furthermore, because of the large degree of variation across languages in specific grammatical structures, descriptions of the underlying “Universal Grammar” (UG) common to all languages are limited to very general descriptions of the phenomena at issue. I have previously described in detail the ways in which published descriptions of the features of UG are fundamentally semantic in nature (Schoenemann, 1999).

For example, Table 1 lists the putative features of UG derived from Pinker and Bloom (1990) and Bickerton (1990). Whenever a particular feature is accomplished differently in various languages, the phrases “mechanisms exist”, “constructions exist”, or “lexical

Table 1
Putative features of Universal Grammar,
according to Pinker and Bloom (1990) and Bickerton (1990).

- A) Hierarchical structure.
- B) Grammatical rules are dependent on this hierarchical structure ('structure dependency').
- C) Lexical categories ("noun," "verb," "adjective," etc.) can be identified because of rules regarding their arrangement.
- D) Individual lexical items are abstract general categories, which are combined in various ways to refer to specific events, things, states, locations, etc..
- E) Rules specify how phrases should be combined, allowing the hearer to decode the underlying relationships between phrases, and hence the underlying meaning intended by the speaker.
- F) Mechanisms exist with allow the hearer to distinguish among various possible argument relationships between the constituent phrases of a sentence.
- G) Mechanisms exist to indicate temporal information.
- H) Verbs take either one, two or three arguments.
- I) Mechanisms exist to convey relations such as truth value, modality and illocutionary force (Steele, et al. 1981).
- J) Mechanisms exist to indicate the relationships between propositions in cases in which one proposition is an argument of another.
- K) Constructions exist to refer to a specific entity simply by specifying its role within a proposition.
- L) Lexical items exist (e.g., anaphoric items such as pronouns) which allow one to repeat a reference to something without having to repeat the entire noun phrase.
- M) Mechanisms exist which license the omission of repeated phrases
- N) Mechanisms exist which allow the fixing of a tightly constrained co-occurrence pattern between an empty element and a sentence-peripheral quantifier.

items exist” are used to indicate this. It is obvious from this list that highly specific rules and constructions are missing. Instead, general characterizations regarding the types of information that grammars universally code are included, rather than the specific rules that are

used to code them. This is because the specific rules themselves are *not* universal. Furthermore, the types of information that grammars universally code can be seen as a reflection of our underlying conceptualization of the world. This raises the question, discussed below, of whether grammar is simply an epiphenomenon of semantics

A few examples will illustrate this point (for a more detailed discussion, see Schoenemann, 1999). All natural language grammars are hierarchically structured (feature A). In a sentence like: “The poem made weak men blush and strong women cry”, we understand that men are weak and blushing, women are strong and crying, and that a poem had this effect on both, and not some other combination of the actions, actors and things mentioned in the sentence. The hierarchical structure of the sentence allows us to unravel these relationships. However, this is clearly a reflection of our underlying conceptual structure. We understand the world in this way. We organize social institutions hierarchically (often without clearly recognizing this as a choice, or even consciously planning them to look like their current state). Conceptual understanding of hierarchical structure is also something that evolved long before humans, and is not a result of language itself (cf., Bickerton, 1990). Primate social relationships are hierarchically structured in various ways (Cheney and Seyfarth, 1990; de Waal, 1989), for example. Furthermore, any complex structure built up from simpler beginnings is likely to be organized hierarchically (Sampson, 1978; Sampson, 1979; Sampson, 1980; Simon, 1962; Wang, 1984), regardless of how we conceptualize the world.

In addition, key differences between sentences (which serve to indicate alterations in meaning) respect this hierarchical structure (this is often referred to as ‘structure dependency’; feature B). For example, the difference between the question “Is the boy who is angry here?” and the related statement “The boy who is angry is here” involves the location of only one of the two verbs in the sentences (plus differences in pitch contours when spoken). The question asks about whether a specific boy (i.e., the one who is angry) is here or not, it does not ask whether the boy is angry. We

know this because the phrase “. . . the boy who is angry” is left unchanged between the two sentences. Thus, exactly where a change or difference occurs in the structure of a sentence indicates what the difference in intended meaning is: phrase structures represent units of conceptual understanding. In the example above, “. . . the boy who is angry . . .” is a complete conceptual unit. Non-structure-dependent grammars would break up these conceptual units, thereby requiring additional complexities to unravel the intended meanings. It does not matter that there are a few cases in which the semantic meaning of a particular unit may not be clear (as with “there” in “Is there any chocolate left?”). What matters is that in the vast majority of cases the structures in question are recognizable conceptual units. These cases form the basis for structure dependency rules, which then get applied even in cases where the meanings of particular units are unclear (for more detailed discussion, see Schoenemann, 1999).

Another feature of all grammars is that they distinguish nouns from verbs (feature C). This clearly reflects the fact that we conceptualize two facets of (our) reality: objects (or ‘things’, defined as loosely as one likes) and actions (acts, occurrences, or modes of being of these objects). Whether or not it is possible to neatly characterize every noun or verb in this way is not critical. It is clearly the core of the distinction — we do in fact conceptualize reality in this way — and we should expect language to reflect this.

In all languages, some mechanism exists for coding argument structure (e.g., who did what to whom; feature F). The mechanism varies, however, such that in some languages each noun is modified to indicate whether it is the direct object, indirect object, and so forth (case markings, as in Latin), while in other languages word order plays a more central role (as in English). Thus, what is universal is not a specific set of rules, but the concept of argument structure itself. Similarly, all languages have some mechanisms for coding temporal information (feature G). In some languages this is accomplished via verb inflection (as in English), while in others the verb does not change and instead temporal information is indicated through the use of separate words (as in Chinese dialects). Again,

what is universal is not the specific rule structure, but simply that the concept of temporal information is coded in some way.

A perusal of the other features in Table 1 indicate that they also are not specific rules, but rather acknowledgements that particular kinds of conceptual information are coded by all natural language grammars. This suggests that the innate structures of language are actually semantic and conceptual, rather than grammatical and syntactic. In other words, it appears there has been a conflation of (1) the fact that grammatical rules exist (though they vary in their specifics), with (2) the fact that some key conceptual features are cross-cultural. Since the specific grammatical structures encoding various universal conceptual frameworks vary from language to language, we must assume these variants are cultural in origin.¹ The cultural evolution of grammar will necessarily involve the creation of structures that reflect underlying conceptual structure, and thus it is not necessary to propose a separate set of innate grammar-specific modules to guide this process. The fundamentally conceptual nature of the description of UG does not in and of itself prove that innate grammar-specific modules do not exist, of course, but it does suggest a more parsimonious proposition: the elaboration of semantic/conceptual complexity during human evolution drove the cultural evolution of grammar.

4.2 Evidence against the innateness of grammar

One of the key arguments for the specific innateness of grammar has

¹ One way around this conclusion would be to argue that a number of alternative grammatical structures are programmed genetically, but the specific features a child will learn are set by exposure to one or another grammatical structure (often referred to as “parameter setting”). I have previously explained why this idea is evolutionarily incoherent (Schoenemann 1999). Essentially, it requires multiple adaptations to the same problem, akin to birds evolving the possibility of growing completely different kinds of wings depending on the environment they find themselves in during development.

been that a child could not possibly learn the correct set of rules for their language on the basis of positive examples only (e.g., Bowerman, 1988; Komarova et al., 2001). Children are not consistently corrected for speech errors (Brown and Hanlon, 1970) and rarely pay attention even when corrected (McNeill, 1966). Because there are an infinite number of possible grammars consistent with any finite set of example sentences, it is logically impossible for a child to determine the actual grammar without some form of constraints on learning (Gold, 1967; Nowak et al., 2001).

However, there are several problems with this argument. First, it isn't at all clear that even most children converge on the same grammar. Instead, given that adult grammaticality judgments vary so much (Ross, 1979), it seems they simply converge on a set of grammars that are "good enough" for communication. Second, positive evidence can actually be used as a weak form of negative evidence (i.e., "if this form is correct, then another is unlikely to be correct, barring future positive evidence to the contrary"). Chomsky (1981) has pointed out that if children notice that "...certain structures or rules fail to be exemplified in relatively simple expressions, where they would be expected to be found, then a (possibly marked) option is selected excluding them in the grammar, so that a kind of 'negative evidence' can be available even without corrections, adverse reactions, etc." (p. 9). Regier (1996) showed that this can be implemented for learning word meanings as well. Third, there is nothing in Gold's (1967) thesis that requires that constraints on learning must be specifically grammatical, or even specifically linguistic. All that is required is that there be constraints of some kind. Thus, the question has really always been "what are the nature of the constraints?" and not "are there any constraints on language learning at all?" Since, as discussed above, descriptions of the major features of UG appear to be essentially descriptions of key parts of our semantic/conceptual worlds, we must seriously consider the possibility that the constraints on UG are actually semantic/conceptual, rather than grammar-specific. In this respect, it is of interest to note that the developmental emergence of grammar

in children is apparently highly correlated with vocabulary size (Bates and Goodman, 1997). If vocabulary size can be seen as a proxy for conceptual complexity, then the connection between grammar and vocabulary development is consistent with the model suggesting that conceptual complexity drives grammatical complexity.

4.3 Lack of syndromes solely affecting syntax or grammar

If grammar and syntax require innate structures that evolved solely for this purpose, it should be possible to find examples of clinical syndromes that only affect them. There are, however, apparently no such cases. It is true that Broca's aphasics can have difficulties with certain kinds of grammatical structures (e.g., passive sentences, although the exact pattern of grammatical deficit appears to vary significantly across subjects) (Caramazza et al., 2001). However, the key question in the present context is whether Broca's aphasia is associated with any non-linguistic deficits. This has, understandably, not been the focus of research attention in Broca's aphasics. However, there is some research suggesting that Broca's aphasics have difficulty with non-linguistic sequential learning (Christiansen et al., 2002). If confirmed, this would suggest that Broca's aphasia is not specifically linguistic, though it obviously does affect language processing in important ways. An evolutionary perspective would predict that the neural substrate underlying Broca's aphasia (as with any area relevant to language processing) would have been derived from pre-existing circuits that happened to process information in ways easy to modify for use in language. Our expectation should be that all 'language' areas will have important non-linguistic functions.

Work on William's syndrome (sometimes offered as evidence of the innateness of grammar, e.g., Pinker, 1994) has not produced a consistent picture of intact linguistic abilities combined with non-linguistic deficits. These individuals are highly retarded (IQ of

~50), but are remarkably verbal. However, Bates (1992) notes that they have other spared abilities as well (e.g., face recognition). Furthermore, they show impairments of lexico-semantics, morphological feature analysis, and at least some syntactic abilities (Karmiloff-Smith et al., 1998).

4.4 Language genes

If grammar is only a reflection of conceptual structure, then genetic influences on grammar will either affect conceptualization more generally, or will affect mechanisms that are not specific solely to language. What little is concretely known at present regarding the genetics of language clearly supports this model, rather than the idea of language-specific genes. Recently a great deal of effort has been focused on a gene known as *FOXP2* (the so-called “language gene”) (Enard et al., 2002). Individuals with a rare variant of this gene show various language deficits, including problems of grammar comprehension and production. Crucially, however, the pattern of deficits does not indicate specificity only to grammar: subjects with this variant show severe articulation difficulties, for example (Alcock et al., 2000; Watkins et al., 2002). Even more problematic, however is that the grammatical problems they exhibit are not even features of Universal Grammar. For example, they have difficulty with tense markers, and verb inflection generally, yet many languages completely lack verb inflection (e.g., all dialects of Chinese, Wang, 1991a). This indicates that *FOXP2*, while it clearly affects language, is *not* evidence for an innately-specified language-specific grammar module. Instead, it fits perfectly with a model in which different languages utilize different pre-existing cognitive components, many of which may well be genetically specified to varying degrees, but none of which evolved solely for language.

5. Grammar and Syntax as Emergent Characteristics of Semantic/Conceptual Complexity

5.1 Sociality and the human condition

To place language, and grammar in particular, into proper context, it is critical that we recognize the fundamentally social nature of the human condition. There are many species which do not live in, or depend on, groups of conspecifics (e.g., bears, tigers). Many other species are found in groups, but are not particularly interactively social (e.g., schools of fish). They group together primarily to decrease their individual likelihood of being preyed upon. However, some species are much more obviously interactively social. Primates (with some exceptions) fall into this category, but humans are arguably the most interactively social of all. It is considered such a fundamental part of human nature that we actually identify, label and try to treat medically people who have problems with social interactions (e.g., autistics), and consider solitary confinement in prison to be one of the worst possible punishments. Much of what we do has been learned specifically through some form of imitation of others. Language is used in large measure, of course, to facilitate social interaction. It is also clear that large parts of language are also learned, rather than innately given. This is obviously true for the specific sound sequences that make up our lexicon, but is also true for all the grammatical peculiarities that are not part of UG.

5.2 Emergence of grammar and syntax

If the universal features of grammar are really just reflections of our internal conceptualization of the world, while the specific rules and structures used by a given language are highly variable and not genetically coded themselves (instead borrowing and possibly elaborating on pre-existing cognitive abilities), and if at the same time the human condition is one of intense interactive sociality in

which learning through some form of imitation is ubiquitous, then an alternative model of the evolution of grammar and syntax may be considered. The specific rules and structures in a given language represent simply conventionalizations that allow languages to accurately communicate human semantics. Grammar and syntax would in this case be seen as behavioral adaptations that take advantage of different possible (i.e., pre-existing) cognitive abilities to accomplish the task of representing higher-order conceptual complexity.

To take a concrete example, consider the use of serial order in some languages to mark argument relationships (Schoenemann and Wang, 1996). While the neural circuits involved in this process have not been identified in any detail, it is known that the prefrontal cortex is involved in marking temporal information generally. Subjects with prefrontal damage cannot plan and execute a complex set of motor movements, program a set of activities in correct temporal order, or remember the order of experiences (Fuster, 1985; Milner et al., 1985; Milner et al., 1991; Squire, 1987; Struss and Benson, 1986). This is true of non-human animals as well. A dissociation between item memory and order memory (with memory of sequential order localized in the frontal lobes) has been demonstrated in monkeys (Petrides, 1991; Squire, 1987) and even rats (Kesner and Holbrook, 1987; Kesner, 1990). The fact that the prefrontal cortex appears to be specifically involved in memory for serial order in species as far removed from humans as rats suggests that this specialization is very old (primate-rodent common ancestry dates to ~65 MYA, Sarich, 1985). Thus, in the earliest pre-linguistic hominids we can be confident that there were circuits already adapted specifically to processing serial information. An evolutionary perspective suggests that these circuits were capitalized upon by increasingly complicated language. The default hypothesis must be that these were adapted to use for language, not that wholly new circuits were created solely for language.

Another profitable way to conceptualize this process is to think of language as a form of symbiont: language itself can be thought of as adapting to the human mind (Christiansen, 1994; Deacon, 1997).

By definition, natural languages that are too difficult for humans to learn would never have come into existence. Since this must have been true of every single hominid population extending back to the very origins of language, we must assume that language has molded itself to the hominid mind as much as the hominid mind has molded itself to allow increasingly sophisticated language.

Over time, there would have been an increase in the complexity of the kinds of things the earliest linguistically-inclined hominids would have wanted to try to communicate. This, in turn, would have led to an increase in the kinds of grammatical forms that became conventionalized (Savage-Rumbaugh and Rumbaugh, 1993). Note that even those who believe that UG is innate still must believe that some (not necessarily conscious) cultural elaboration occurred. The question is really over the extent to which this happened, not whether it happened at all.

5.3 Evolution of semantic/conceptual complexity

If grammar is driven by semantic/conceptual complexity, what kind of evidence is there that semantic/conceptual complexity increased during human evolution? Ape language-learning studies suggest that vocabulary sizes of perhaps ~400 words are possible given a human-like developmental environment (Gardner and Gardner, 1989; Miles, 1990; Premack and Premack, 1972; Savage-Rumbaugh et al., 1993). This is at least two orders of magnitude smaller than that reported for the typical high-school senior (Miller and Gildea, 1991). It is not clear, however, how much of this difference is attributable to an underlying difference in semantic/conceptual complexity, rather than some other explanation (such as some inherent difficulty in connecting concepts with arbitrary signs). However, there is another ape/human difference which strongly points toward a difference in conceptual complexity: overall brain size. The human brain is 3–4 times the size of that found in apes, even though apes are similar in body size (gorillas even being quite a bit larger, Deacon, 1992; Falk, 1987; Holloway, 1995; Jerison, 1973). Jerison (1985) has argued that brain size is an index of the

degree of sophistication of an animal's internal representation of the world: "Grades of encephalization presumably correspond to grades of complexity of information processing. These, in turn, correspond in some way to the complexity of the reality created by the brain, which may be another way to describe intelligence." (p. 30). There are several reasons to suspect that this is in fact correct, and that the human difference indicates a major increase in conceptual complexity.

First, concepts are instantiated in the brain as webs or networks of activation between primary sensory, secondary and association areas. This is directly evident from functional imaging studies of various kinds (see Pulvermuller, 2001), as well as behavioral work on correlations between word meanings (McRae et al., 1997). Functional imaging studies of people trying to imagine objects have shown that essentially the same patterns of activity are evident when people are imagining an image as when they are actually viewing it (Damasio et al., 1993; Kosslyn et al., 1993). These studies also demonstrate that information flows bi-directionally: activation of primary sensory areas is dependent not just on inputs from external sensors, but can occur purely as a result of inputs internally from other areas of the brain.

It is also clear that most of our subjectively experienced concepts are actually complex combinations of sensory information processed in various ways by the different cortical centers. This is clear for concepts like "ball," or "fear," which elicit an array of sensory information (e.g., "ball" has visual and sensorimotor components; "fear" has various visual, auditory, sensorimotor, and limbic components). But it is also true of apparently relatively simple concepts. It turns out that our experience of taste is actually the result of the interaction of olfactory (smell) and gustatory (taste) inputs. This can be easily demonstrated by eating a banana while alternately holding one's nose closed and opening it. The banana "flavor" disappears when the nose is blocked, because it is actually largely olfactory. The "McGurk" effect (McGurk and MacDonald, 1976), in which the auditory perception of a phoneme can be altered if it is paired with a mismatched visual input, similarly indicates that

conceptual awareness is the result of complex interactions between different inputs. This means there must be networks connecting differing regions as well as areas that mediate the integration of this information.

To what extent is brain size relevant to conceptual complexity? It is certainly reasonable to suppose that larger brained species have more complicated networks of interconnection, thereby leading to greater potential conceptual complexity (Lieberman, 2002). However, strong support for this idea comes from a consideration of brain structure/function relationships across species. It is well known that behaviorally specialized animals have correlated increases in areas of the brain known to mediate those behaviors (e.g., Krubitzer, 1995). For example, over half of the cortex of the echolocating ghost bat (*Macroderma gigas*) is devoted to processing auditory information, and approximately two-thirds of the cortex of the platypus (*Ornithorhynchus anatinus*) is devoted to processing electrosensory and mechanosensory information from its highly specialized bill (Krubitzer, 1995). The blind mole rat (*Spalax ehrenbergi*) spends essentially its entire life underground, placing somatosensory information at a premium, and making visual information useless. This species devotes a much larger portion of its cortex to somatosensory processing than rodents generally, while at the same time completely lacking a visual cortex (Mann et al., 1997). Racoons (*Procyon lotor*) display highly developed manual dexterity, and their somatosensory cortex is concomitantly relatively large for carnivores — to the extent that individual digits are represented on distinct cortical gyri (Krubitzer, 1995). Furthermore, it has even been shown that selective breeding for more whiskers in mice leads to an increase in the cortical representation of the somatosensory area corresponding to whiskers (Van der Loos et al., 1986). In fact, detailed mapping shows that each additional whisker is assigned its own additional cortical field (Van der Loos et al., 1986).

These studies show that increased behavioral complexity is associated with increased neural resources. While we do not yet have detailed studies of the actual network complexity (i.e., circuit

diagrams) in these species, it is a reasonable assumption that the increase in neural resources is an index of an increase in fundamental network complexity.

In addition to the general association between brain region size and behavioral specialization, it appears that larger brained animals have greater degrees of cortical specialization. There appear to be basic structural constraints that influence changes in neural connectivity in important ways, which in turn are likely to have fundamental effects on conceptual complexity. Larger brains have more neurons (Haug, 1987), but in order for these neurons to remain equally well connected with each other (in the sense of a signal having the same average number of synapses to traverse between any two neurons), the number of connections (axons) must increase much faster than the number of neurons (Ringo, 1991). Comparative data from Hofman (1985) on volumes of white and grey matter (which is composed primarily of neuron cell bodies and associated glial support cells) shows that white matter in fact increases faster than grey matter with increasing brain size. However, the increase is apparently not fast enough to maintain equal degrees of connectivity between neurons (Ringo, 1991). This means that as brain size increases, there is a concomitant increase in the separation between existing areas.

There are a number of comparative studies that highlight this process. One particularly interesting example involves the separation of the motor and somatosensory areas of the cortex. In humans, as for primates generally, these two areas are separate. However, in opossum the areas appear to be completely overlapping. In rats, only the forelimbs have separate motor and somatosensory cortical representations; the hindlimbs match the opossum pattern (Ebbesson, 1984). Having separate motor and somatosensory areas presumably allows for a more complicated response to a given sensory input. Motor processing may proceed with greater independence of sensory input in primate brains compared to opossum brains.

Another example of this pattern occurs in the connections between visual and motor cortex, in which smaller-brained animals

such as rats and mice have direct projections from their primary visual cortex to their primary motor cortex, whereas the much larger-brained anthropoid primates lack such direct projections (Northcutt and Kaas, 1995). This allows for a greater sophistication of processing of visual information before a motor action is taken.

Detailed comparative studies of cortical areas confirm that larger brained species have a greater number of distinct cortical areas than smaller brained species (Northcutt and Kaas, 1995). For example, rodents have only 5–8 visual areas (Northcutt and Kaas, 1995), whereas primates appear to have perhaps 20–30 (Felleman and Van Essen, 1991; Northcutt and Kaas, 1995). Thus, empirical evidence shows that increasing brain size leads to increasing numbers of cortical areas, and increasing independence of these cortical areas. Cortical specialization is critical to conceptual complexity because it increases the potential ability to differentiate complex sensory information into diverse constituent parts. It is easy to see how these parts would help to magnify subtle differences between different streams of sensory input, thereby clarifying what would otherwise be inchoate. Given the large, obvious evolutionary costs of increasing neural tissue (Hofman, 1983; Smith, 1990), and the consequent impossibility of explaining brain size increases short of some sort of adaptive benefit, the best explanation would appear to be increasing conceptual complexity.

At a more general level of behavior and anatomy, it is known that brain size is associated with differences in social complexity (Dunbar, 1992; Dunbar, 1995; Sawaguchi, 1988; Sawaguchi, 1990; Sawaguchi and Kudo, 1990), degree of innovation, social learning, tool use (Reader and Laland, 2002), and even rates of apparent deceptive behavior (scaled by the number of studies done on different species, Byrne, 1993). All of this suggests that increasing brain size is an index of increasing cognitive (and therefore conceptual) complexity.

5.4 Evolutionary simulations

Since evolutionary dynamics generally occur over a long time scale,

and have to be inferred from limited data, computer simulations of various kinds are useful tools for testing particular evolutionary models. The acquisition and emergence of vocabulary in populations of interacting agents has been studied in this way, leading to insights into possible evolutionary dynamics (Ke et al., 2002). A number of recent simulation studies have shown that the cultural emergence of grammar can be computationally modeled using agent-based simulations (e.g., Batali, 1998; Brighton and Kirby, 2001; Kirby, 2000). These models start with agents that do not have UG hardwired into them *per se*, but instead have simply general learning and pattern-matching algorithms. They are also required to communicate with one another, though they do not necessarily need to agree about which sets of symbols should be used for which concepts. While they clearly only model parts of the complete story, they nevertheless indicate that intuitions about what sorts of innate structures are necessary for UG-like features to emerge are, at the very least, suspect.

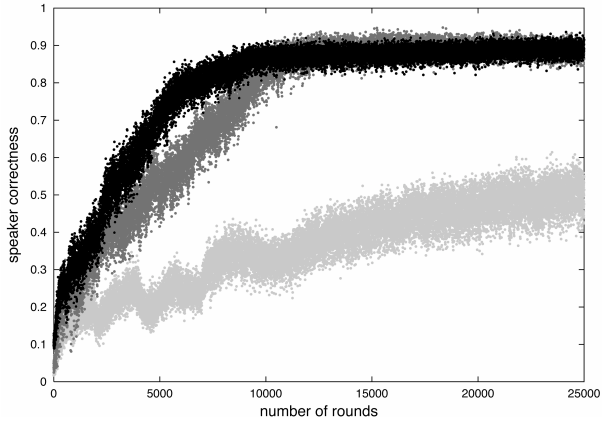
One feature that has not been extensively studied in these agent-based studies is the relationship between brain size (general cognitive capacity) and conceptual complexity. To what extent is it possible to show that larger brain size has any relevance to increasing conceptual complexity, particularly in the context of a model of communication among agents? To address this question, Craig Martell (formerly of the Computer Science Department at the University of Pennsylvania, now at RAND) and I modified a simulation involving populations of interacting artificial neural nets. This particular simulation had been introduced originally by Batali (1998), and had been rewritten in the LISP programming language by Goroll (1999). The basic structure of the simulation is as follows. 30 virtual agents are constructed, each one composed of a single recurrent neural net (Elman, 1990). These nets each have 4 input nodes, 30 hidden nodes, and 10 output nodes. The recurrent feature of the nets means that the hidden nodes are ‘copied back’ each cycle and are used as additional inputs (such that there are actually 30 recurrent + 4 new inputs each cycle). Each agent ‘knows’ the same 100 meanings: all the possible combinations of 10 referents and 10

predicates (e.g., ‘you angry’, ‘you excited’, ‘me angry’, etc.). ‘Words’ are produced by choosing a target meaning at random and finding the sequence of letters (introduced one at a time to the new input nodes) such that the output meaning vector of the ‘speaking’ agent most closely matches the target meaning. This input sequence is then given to a ‘hearer’ along with the original intended meaning.² In each round, one agent is taught (i.e., its net is adjusted via standard backpropagation algorithms) to better understand 10 other agents’ words for each of their meanings (for details see Goroll, 1999). In Batali’s original simulation the population converged on a common code after about 15,000 rounds. Furthermore, the common code included strong suggestions of compositionality.

For our simulations, two types of modifications were made. First, simulations were run using agents with either 100 meanings (as in the original simulation) or 200 meanings. Second, the sets of agents were given either 15, 30 or 60 hidden units, simulating simple changes in ‘brain’ size. The question we were interested in addressing was the extent to which the size of the artificial neural net affected the ability of the population to converge on a common code. Figure 2 shows the change for populations of agents with 100 meanings in average ‘speaker correctness’, which is the degree to which a speaker’s output (meaning) nodes match the intended (randomly chosen) meaning after the best input sequence is determined. The simulations using populations of agents with 15, 30, and 60 hidden nodes are plotted together. Figure 3 shows the same information, but this time with agents who have 200 possible meanings. It is clear from both figures that populations of nets with larger numbers of hidden units evolve more complicated languages faster and with less error than populations with smaller numbers of hidden units. This is, to some extent, not surprising. It is generally

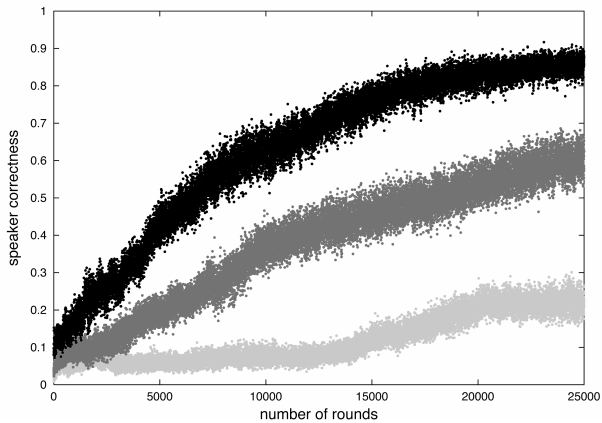
² This obviously involves something of a cheat, in that perfect knowledge is assumed between speaker and hearer. However, there must be some way in which intended meanings are indicated, e.g., from parent to child, among humans.

Figure 2
Rates of convergence to a common code for 100 meanings.



Change in 'speaker correctness' for three populations of agents, each knowing 100 possible meanings. Light grey: agents with 15 nodes ('neurons') in the hidden layer; dark grey: agents with 30 nodes; black: agents with 60 nodes.

Figure 3
Rates of convergence to a common code for 200 meanings.



Change in 'speaker correctness' for three populations of agents, this time with each agent knowing 200 possible meanings.

known that nets with larger hidden layers can learn more complicated types of associations than nets with smaller hidden layers. Nevertheless, this simulation is useful in showing that the principle applies equally to populations of interacting agents. To the extent that artificial neural nets model important aspects of real neural nets appropriately, this simulation also demonstrates at a basic level the idea that larger brains would be a likely concomitant of increasing semantic complexity. Future ideas to be pursued include adding a more sophisticated and realistic learning process (in which ‘hearers’ don’t have perfect knowledge of the intended meanings), increasing meanings in a more interesting and realistic way (e.g., in which different dimensions of meaning are added, rather than simply more of the same basic type), analyzing the effects of net size on compositionality, and devising a better learning process that doesn’t bias sequences toward the smallest possible length (which tends to work against full compositionality, particularly if the nets are large enough to simply memorize large numbers of individual sequences).

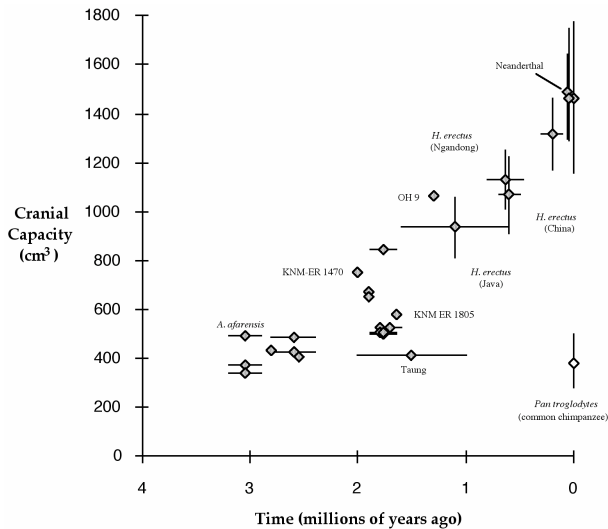
5.5 Implications for the evolution of language

Whatever else increasing brain size led to in hominid evolution, it is difficult to escape the conclusion that conceptual complexity increased substantially during this time. Given the fundamentally socially interactive nature of humans, as well as the general association between degree of sociality and brain size, it is likewise difficult to believe that this increase in conceptual complexity could be unrelated to the evolution of language. The idea that the evolution of brain size and language are somehow related has a long history (e.g., Dunbar, 1996; Nadeau, 1991; Wang, 1991b; Washburn, 1960). Darwin himself (1882) argued for “. . . the relation between the continued use of language and the development of the brain . . .” (p. 87).

This suggests that brain size itself may be an index of language evolution. If so, it would suggest that language has origins that are

substantially older than the appearance of anatomically modern *Homo sapiens*, which date to only ~100,000 years ago (Tattersall, 1998). Figure 4 shows the change in hominid cranial capacity (a good proxy for brain size) over the last four millions years for the majority of the fossil specimens that have been measured. It is evident that the major shift in brain size toward the modern condition began sometime between two and three million years ago. The earliest evidence for stone modification (presumably for tool use) is also found in this time range.

Figure 4
Cranial capacity in fossil hominids over time.



Species names are in italics; other labels refer to individual specimens. Extant chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) are included for comparison. Horizontal bars reflect uncertainties in dating. Vertical bars indicate ranges in cranial capacity for given taxonomic groupings (data points without vertical bars indicate single specimens). Data compiled by Falk (1987), with minor changes (Schoenemann, 1997)

There are a number of proponents of a relatively late date for the origin for language (at least for completely modern, fully

syntactic language, e.g., Bickerton, 1995; Klein and Edgar, 2002; Tattersall, 1998). Their arguments rely heavily on a postulated tight connection between apparently sharp increases in the incidence of art and other forms of material culture in the archaeological record that are evident starting at around ~35,000 years ago. The implication that language must be reflected in material culture is, however, inherently problematic (Dibble, 1987). There is a tremendous range of variation in the complexity of material culture left behind by different modern human groups, yet all have fully modern language. Material culture obviously can change dramatically without requiring fundamental changes in language. It thus remains purely speculative to suggest that fully modern syntactic language explains the Middle to Upper Paleolithic transition. These models also, it is important to note, generally argue that some form of communicative behavior was likely evident prior to this point (Bickerton, 1995; Klein and Edgar, 2002).

There are, in fact, suggestions that hint toward a much older date of origin. One line of argument derives from studies of the basicranium of various fossil hominid specimens (Laitman, 1983; Laitman, 1985; Lieberman, 1984), which, it is argued, allow estimates of the extent to which the larynx had lowered from the ape condition, thereby allowing for a significantly greater range of vowel sounds. Since it would presumably also have increased the likelihood of choking on food, it would not have happened without some adaptive benefit which is assumed to be language (but see Fitch and Reby, 2001). While it is true that this work suggests that Neanderthals (known from ~120,000 to ~35,000 years ago) did not have a fully lowered larynx, fossils even older than this appear to have a lower larynx than Neanderthal specimens. To the extent that this work can accurately estimate laryngeal position, it actually suggests that the lowering of the larynx had begun at least as far back as *Homo erectus*, about ~1.5 million years ago (Laitman, 1985).

Other suggestive evidence for an early origin comes from studies of the endocasts of early hominids. At least one specimen, KNM-ER 1470 (*Homo habilis*), dating to ~1.8 million years ago, has been

claimed to have a sulcal pattern in the inferior frontal region (which includes the area where Broca's area is located) that most closely matches modern humans rather than modern apes (Falk, 1983). This does not, of course, prove that *Homo habilis* had a Broca's area, nor that it had language, however.

Two other suggestions have been made in recent years regarding date of the origin of language. One involves the possibility that narrow vertebral canals in one specimen of *Homo erectus* (KNM-WT 15000) indicate a lack of sophisticated control over the muscles involved in controlling sub-laryngeal air pressures, and hence a lack of language in this species (Walker and Shipman, 1996). However, this has recently been questioned on the grounds that the specimen appears pathological (Latimer and Ohman, 2001; Meyer, 2003) and that intercostal muscles do not play a significant role in language production (Meyer, 2003). Another suggestion has been that the relatively large size of the hypoglossal canal (which carries the nerves to most of the muscles that control the tongue) in some later *Homo erectus* specimens may indicate the presence of language in these specimens (Kay et al., 1998). However, this has also been questioned on the grounds that there is no clear evidence that the size of the canal is an index of the degree of motor control of the tongue, as well as that the range of hypoglossal canal size in modern humans overlaps substantially with that of other non-human primates (DeGusta et al., 1999).

Thus, while the evidence is clearly equivocal, there would appear to be reasonable evidence of a long history of language in hominid evolution. The evidence of the relationship between brain size and conceptual complexity suggests, at a minimum, that fundamental changes in human cognition critical to language evolution had begun prior to ~2 million years ago.

6. Conclusions

Evolutionary change is biased towards modification of pre-existing mechanisms, and away from the construction of wholly new devices.

This means that we should look for evidence of continuity, regardless of how unique a particular adaptation might appear. A review of the evidence available to date suggests there are in fact many areas of continuity. The aspect of language in which continuity is least evident is in syntax and grammar. However, since the universal features of grammar are essentially descriptions of aspects of our basic conceptual universe, while the specific rules vary from language to language, the most parsimonious model is that increasing conceptual/semantic complexity drove the acquisition of syntax and grammar (which would then be cultural manifestations of this pre-linguistic internal conceptual universe). An understanding of the way in which concepts are instantiated in the brain, combined with a comparative perspective on brain structure/function relationships, indicates that increasing brain size during hominid evolution reflects an increase in conceptual complexity. It is possible to simulate this process at a simple level with populations of interacting artificial neural-net agents. All of this suggests that the origins of language have a deep ancestry.

Acknowledgments

I am indebted to Professor William S.-Y. Wang not only for making it possible for me to participate in the ACE workshops, but for profoundly shaping my views on language evolution through his many contributions to this area of inquiry. This paper has also benefited from discussions with the many participants of the workshops, particularly Professor Wang, Professor Thomas Lee, Professor Morten Christiansen, Craig Martell, Jinyun Ke, James Minett, Ching Pong Au, and Feng Wang. In addition, the ideas in this paper have been shaped over the years by many discussions with Professor Vincent Sarich, Dr. John Allen, Dr. Karen Schmidt, and Reina Wong. I am particularly indebted to Craig Martell, now at RAND, for his intellectual contribution and programming expertise on the agent-based simulations described in this paper. Lastly, I would like to thank the City University of Hong Kong for graciously hosting the ACE workshops and helping make the events so productive, and to the University of Pennsylvania for their sponsorship.

References

- Agha, Asif. 1997. 'Concept' and 'communication' in evolutionary terms. *Semiotica*, 116.189–215.
- Alcock, K. J., Passingham, R. E., Watkins, K. E. and Vargha-Khadem, F. 2000. Oral dyspraxia in inherited speech and language impairment and acquired dysphasia [Oct 15]. *Brain and Language*, 75.17–33.
- Batali, J. 1998. Computational Simulations of the Emergence of Grammar. *Approaches to the Evolution of Language: Social and Cognitive Bases*, ed. by J. R. Hurford, M. Studdert-Kennedy and C. Knight, 405–26. Cambridge: Cambridge University Press.
- Bates, Elizabeth. 1992. Language development. *Current Opinion in Neurobiology*, 2.180–85.
- Bates, Elizabeth and Goodman, Judith C. 1997. On the inseparability of grammar and the lexicon: Evidence from acquisition, aphasia, and real-time processing. *Language & Cognitive Processes*, 12.507–84.
- Bickerton, Derek. 1990. *Language & Species*. Chicago: University of Chicago Press.
- . 1995. *Language and Human Behavior*. Seattle: University of Washington Press.
- Bowerman, Melissa. 1988. The 'no negative evidence' problem: How do children avoid constructing an overly general grammar? *Explaining Language Universals*, ed. by John A. Hawkins, 73–101. New York: Basil Blackwell Inc.
- Brighton, Henry and Kirby, Simon. 2001. The survival of the smallest: stability conditions for the cultural evolution of compositional language. *Advances in artificial life: Proceedings of the 6th European Conference, ECAL 2001*, 592–601. New York: Springer.
- Brown, R. and Hanlon, C. 1970. Derivational complexity and order of acquisition of syntax. *Cognition and the Development of Language*, ed. by J. R. Hayes, 11–53. New York: Wiley.
- Byrne, Richard. 1993. Do larger brains mean greater intelligence? *Behavioral and Brain Sciences*, 16.696–7.
- Capranica, R. R. 1965. *The Evoked Vocal Response of the Bullfrog*. Cambridge, Mass.: MIT Press.
- Caramazza, A., Capitani, E., Rey, A. and Berndt, R. S. 2001. Agrammatic Broca's aphasia is not associated with a single pattern of comprehension performance [Feb]. *Brain and Language*, 76.158–84.
- Carpenter, Malcom B. and Sutin, Jerome. 1983. *Human Neuroanatomy*. Baltimore, Maryland: Williams & Wilkins.

- Cheney, Dorothy L. and Seyfarth, Robert M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behavior*, 36.477–86.
- Cheney, Dorothy L. and Seyfarth, Robert M. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.
- Chomsky, Noam. 1972. *Language and Mind*. New York: Harcourt Brace Jovanovich, Inc.
- . 1981. *Lectures on Government and Binding*. Dordrecht: Foris Publications.
- Christiansen, Morten H. 1994. *Infinite Languages, Finite Minds: Connectionism, Learning and Linguistic Structure*, University of Edinburgh: Unpublished PhD dissertation.
- Christiansen, Morten H., Dale, Rick A., Ellefson, Michelle R. and Conway, Christopher M. 2002. The role of sequential learning in language evolution: Computational and experimental studies. *Simulating the evolution of language*, ed. by Angelo Cangelosi and Domenico Parisi, 165–87. New York: Springer-Verlag Publishing.
- Croft, William 1991. *Syntactic categories and grammatical relations*. Chicago: University of Chicago Press.
- Croft, William. 2003. *Typology and universals*. Cambridge: Cambridge University Press.
- Damasio, H., Grabowski, T. J., Damasio, A., Tranel, D., Boles-Ponto, L., Watkins, G. L. and Hichwa, R. D. 1993. Visual recall with eyes closed and covered activates early visual cortices. *Society for Neuroscience Abstracts*, 19.1603.
- Darwin, Charles. 1882. *The Descent of Man and Selection in Relation to Sex*, 2nd Edition. London: John Murray.
- de Waal, Frans. 1989. *Peacemaking Among Primates*. Cambridge: Harvard University Press.
- Deacon, Terrence W. 1984. *Connections of the Inferior Periarculate Area in the Brain of Macaca fascicularis: An Experimental and Comparative Investigation of Language Circuitry and its Evolution*: Harvard University: Unpublished PhD dissertation.
- . 1988. Human brain evolution: I. Evolution of language circuits. *Intelligence and Evolutionary Biology*, ed. by H. J. Jerison and I. Jerison, 363–82. Berlin: Springer-Verlag.
- . 1989. The neural circuitry underlying primate calls and human language. *Human Evolution*, 4.367–401.
- . 1992. Brain-language Coevolution. *The Evolution of Human Languages*, ed. by J. A. Hawkins and M. Gell-Mann, 49–83. Redwood City, CA: Addison-Wesley.

- Deacon, Terrence W. 1997. *The symbolic species: the co-evolution of language and the brain*. New York: W.W. Norton.
- DeGusta, D., Gilbert, W. H. and Turner, S. P. 1999. Hypoglossal canal size and hominid speech. *Proceedings of the National Academy of Sciences USA.*, 96.1800–4.
- Denes, Peter B. and Pinson, Elliot N. 1963. *The Speech Chain*. Garden City, New York: Anchor Press/Doubleday.
- Dibble, Harold L. 1987. Middle Paleolithic symbolism: a review of current evidence and interpretations. *Journal of Anthropological Archaeology*, 263–96. New York.
- Dittus, W. P. J. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behavior*, 32.470–77.
- Divenyi, P. D. and Sachs, R. M. 1978. Discrimination of time intervals bounded by tone bursts. *Perceptual Psychophysics*, 24.429–36.
- Dunbar, Robin I. M. 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 20.469–93.
- . 1995. Neocortex size and group size in primates: A test of the hypothesis. *Journal of Human Evolution*, 28.287–96.
- . 1996. *Grooming, Gossip and the Evolution of Language*. London: Faber and Faber.
- Ebbesson, Sven O. E. 1984. Evolution and ontogeny of neural circuits. *Behavioral and Brain Sciences*, 7.321–66.
- Elman, Jeffrey L. 1990. Finding structure in time. *Cognitive Science*, 14.179–211.
- Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S., Wiebe, V., Kitano, T., Monaco, A. P. and Paabo, S. 2002. Molecular evolution of *FOXP2*, a gene involved in speech and language [Aug 22]. *Nature*, 418.869–72.
- Falk, Dean. 1983. Cerebral cortices of East African early hominids. *Science*, 221.1072–74.
- . 1987. Hominid Paleoneurology. *Annual Review of Anthropology*, 16.13–30.
- Felleman, D. J. and Van Essen, D. C. 1991. Distributed hierarchical processing in the primate cerebral cortex [Jan-Feb]. *Cereb Cortex*, 1.1–47.
- Fitch, W. T. and Reby, D. 2001. The descended larynx is not uniquely human [Aug 22]. *Proceedings of the Royal Society of London. B, Biological Sciences*, 268.1669–75.
- Fouts, R. S., Chown, B. and Goodin, L. 1976. Transfer of signed responses in American Sign Language from vocal English stimuli to physical object stimuli by a chimpanzee (Pan). *Learning and Motivation*, 7.458–75.

- Fuster, J. M. 1985. The prefrontal cortex, mediator of cross-temporal contingencies. *Human Neurobiology*, 4.169–79.
- Galaburda, A. M. and Pandya, D. N. 1982. Role of architectonics and connections in the study of primate brain evolution. *Primate Brain Evolution*, ed. by E. Armstrong and D. Falk, 203–17: Plenum Press.
- Gardner, R. A. and Gardner, B. T. 1984. A vocabulary test for chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*, 98.381–404.
- . 1989. Early signs of language in cross-fostered chimpanzees. *Human Evolution*, 4.337–65.
- Gold, E. M. 1967. Language identification in the limit. *Information and Control*, 10.447–74.
- Goroll, Nils. 1999. (*The Deep Blue*) Nile: Neuronal Influences on Language Evolution, University of Edinburgh: Master's thesis.
- Haug, H. 1987. Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: A stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores, and one elephant). *American Journal of Anatomy*, 180.126–42.
- Hauser, Marc D. and Wrangham, Richard W. 1987. Manipulation of food calls in captive chimpanzees. *Folia Primatologia*, 48.207–10.
- Hauser, Marc D., Chomsky, Noam and Fitch, W. Tecumseh. 2002. The faculty of language: what is it, who has it, and how did It evolve? *Science*, 298.1569–79.
- Herrnstein, Richard J. 1979. Acquisition, generalization, and discrimination reversal of a natural concept. *Journal of Experimental Psychology*, 5.116–29.
- Hofman, Michel A. 1983. Energy metabolism, brain size, and longevity in mammals. *Quarterly Review of Biology*, 58.495–512.
- . 1985. Size and shape of the cerebral cortex in mammals: I. The cortical surface. *Brain, Behavior and Evolution*, 27.28–40.
- Holloway, Ralph L. 1995. Toward a synthetic theory of human brain evolution. *Origins of the Human Brain*, ed. by Jean-Pierre Changeux and Jean Chavaillon, 42–54. Oxford: Clarendon Press.
- Jackendoff, Ray. 1994. *Patterns in the mind: language and human nature*. New York: Basic Books.
- Jacob, François. 1977. Evolution and tinkering. *Science*, 196.1161–66.
- Jerison, H. J. 1973. *Evolution of the Brain and Intelligence*. New York: Academic Press.
- . 1985. Animal intelligence as encephalization. *Philosophical Transactions of the Royal Society of London, Series B*, 308.21–35.

- Jürgens, Uwe and Zvirner, Petra. 2000. Individual hemispheric asymmetry in vocal fold control of the squirrel monkey. *Behavioural Brain Research*, 109.213–17.
- Karmiloff-Smith, A., Tyler, L. K., Voice, K., Sims, K., Udwin, O., Howlin, P. and Davies, M. 1998. Linguistic dissociations in Williams syndrome: evaluating receptive syntax in on-line and off-line tasks. *Neuropsychologia*, 36.343–51.
- Kay, Richard F., Cartmill, Matt and Balow, Michelle. 1998. The hypoglossal canal and the origin of human vocal behavior. *Proceedings of the National Academy of Sciences USA*, 95.5417–19.
- Ke, Jinyun, Minett, James, Au, Ching-Pong and Wang, William S.-Y. 2002. Self-organization and selection in the emergence of vocabulary. *Complexity*, 7.41–54.
- Kesner, R. P. and Holbrook, T. 1987. Dissociation of item and order spatial memory in rats following medial prefrontal cortex lesions. *Neuropsychologia*, 25.653–64.
- Kesner, Raymond P. 1990. Memory for frequency in rats: Role of the hippocampus and medial prefrontal cortex. *Behavioral and Neural Biology*, 53.402–10.
- Kingston, John. 1991. Five exaptations in speech: Reducing the arbitrariness of the constraints on language. *Behavioral and Brain Sciences*, 13.738–39.
- Kirby, Simon. 2000. Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. *The Evolutionary Emergence of Language*, ed. by Chris Knight, Michael Studdert-Kennedy and James R. Hurford, 303–23. Cambridge: Cambridge University Press.
- Klatt, D. H. and Stefanski, R. A. 1974. How does a mynah bird imitate human speech? *Journal of the Acoustical Society of America*, 55.822–32.
- Klein, Richard G. and Edgar, Blake. 2002. *The Dawn of Human Culture*. New York: John Wiley & Sons.
- Kluender, D. R., Diehl, R. L. and Killeen, P. R. 1987. Japanese quail can learn phonetic categories. *Science*, 237.1195–97.
- Komarova, N. L., Niyogi, P. and Nowak, M. A. 2001. The evolutionary dynamics of grammar acquisition [Mar 7]. *J Theor Biol*, 209.43–59.
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., Hamilton, S. E., Rauch, S. L. and Buonanno, F. S. 1993. Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience*, 5.263–87.
- Krubitzer, Leah. 1995. The organization of neocortex in mammals: are species differences really so different? *Trends in Neurosciences*, 18.408–17.
- Kuhl, Patricia K. and Padden, D. M. 1982. Enhanced discriminability at the

- phonetic boundaries for the voicing feature in macaques [Dec]. *Perceptual Psychophysics*, 32.542–50.
- . 1983. Enhanced discriminability at the phonetic boundaries for the place feature in macaques [Mar]. *Journal of the Acoustical Society of America*, 73.1003–10.
- Kuhl, Patricia K. 1986. Theoretical contributions of tests on animals to the special-mechanisms debate in speech. *Experimental Biology*, 45.233–65.
- Kuhl, Patricia K. and Miller, J. D. 1975. Speech perception by the chinchilla: Voiced-voiceless distinction in alveolar plosive consonants. *Science*, 190.69–72.
- . 1978. Speech perception by the chinchilla: Identification functions for synthetic VOT stimuli. *Journal of the Acoustical Society of America*, 63.905–17.
- Laitman, Jeffrey T. 1983. The evolution of the hominid upper respiratory system and implications for the origins of speech. *Glossogenetics: The Origin and Evolution of Language. Proceedings of the International Transdisciplinary Symposium on Glossogenetics*, ed. by Eric de Grolier, 63–90. Paris: Harwood Academic Publishers.
- . 1985. Evolution of the hominid upper respiratory tract: The fossil evidence. *Hominid Evolution: Past, Present and Future*, ed. by Phillip V. Tobias, Valerie Strong and Heather White, 281–86. New York: Alan R. Liss.
- Lakoff, George. 1987. *Women, Fire, and Dangerous Things*. Chicago: University of Chicago Press.
- Langacker, Ronald W. 1987. *Foundations of Cognitive Grammar. Vol. 1*. Stanford: Stanford University Press.
- Latimer, Bruce and Ohman, James C. 2001. Axial dysplasia in *Homo erectus*. *Journal of Human Evolution*, 40.A12.
- Liberman, Alvin M., Harris, Katherine Safford, Hoffman, Howard S. and Griffith, Belver C. 1957. The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology*, 54.358–68.
- Lieberman, Philip. 1984. *The Biology and Evolution of Language*. Cambridge, Massachusetts: Harvard University Press.
- . 1988. Language, intelligence, and rule-governed behavior. *Intelligence and Evolutionary Biology, NATO ASI Series, Vol. G17*, ed. by H. J. Jerison and I. Jerison, 143–56. Berlin: Springer-Verlag.
- . 2002. On the nature and evolution of the neural bases of human language. *Yearbook of Physical Anthropology*, 45.36–62.
- Mann, M. D., Rehkamper, G., Reinke, H., Frahm, H. D., Necker, R. and Nevo,

- E. 1997. Size of somatosensory cortex and of somatosensory thalamic nuclei of the naturally blind mole rat, *Spalax ehrenbergi*. *Journal für Hirnforschung*, 38.47–59.
- Marler, P., Dufty, A. and Pickert, R. 1986a. Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Animal Behavior*, 34.188–93.
- . 1986b. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behavior*, 34.194–98.
- Mattingly, I. G., Liberman, A. M., Syrdal, A. K. and Halwes, T. 1971. Discrimination in speech and non-speech modes. *Cognitive Psychology*, 2.131–57.
- Mayr, Ernst. 1978. Evolution. *Sci. Am.*, 239.47–55.
- McGurk, H. and MacDonald, J. 1976. Hearing lips and seeing voices [Dec 23–30]. *Nature*, 264.746–8.
- McNeill, D. 1966. Developmental psycholinguistics. *The Genesis of Language: A Psycholinguistic Approach*, ed. by F. Smith and G. Miller, 15–84. Cambridge, Mass.: MIT Press.
- McRae, Ken, de Sa, Virginia R. and Seidenberg, Mark S. 1997. On the nature and scope of featural representations of word meaning. *Journal of Experimental Psychology: General*, 126.99–130.
- Meyer, Marc R. 2003. Vertebrae and language ability in early hominids. Paper presented at Annual Meeting of the PaleoAnthropology Society, Tempe, Arizona.
- Miles, H. Lyn White. 1990. The cognitive foundations for reference in a signing orangutan. “*Language and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*”, ed. by Sue Taylor Parker and Kathleen Rita Gibson, 511–39. Cambridge: Cambridge University Press.
- Miller, George A. and Gildea, Patricia M. 1991. How children learn words. *The Emergence of Language: Development and Evolution*, ed. by William S-Y. Wang, 150–58. New York: W. H. Freeman.
- Miller, P. E. and Murphy, C. J. 1995. Vision in dogs [Dec 15]. *J Am Vet Med Assoc*, 207.1623–34.
- Milner, B., Petrides, M. and Smith, M. L. 1985. Frontal lobes and the temporal organization of memory. *Human Neurobiology*, 4.137–42.
- Milner, Brenda, Corsi, Philip and Leonard, Gabriel. 1991. Frontal-lobe contribution to recency judgements. *Neuropsychologia*, 29.601–18.
- Miyawaki, K., Strange, W., Verbrugge, R., Liberman, A. M., Jenkins, J. J. and Fujimura, O. 1975. An effect of linguistic experience: The discrimination of /r/ and /l/ by native speakers of Japanese and English. *Perceptual Psychophysics*, 18.331–40.

- Morse, P. A. and Snowden, C. T. 1975. An investigation of categorical speech discrimination by rhesus monkeys. *Perceptual Psychophysics*, 17.9–16.
- Nadeau, R. 1991. *Minds, Machines and Human Consciousness*. Chicago: Contemporary Books.
- Negus, V. E. 1949. *The Comparative Anatomy and Physiology of the Larynx*. New York: Hafner.
- Neitz, J., Geist, T. and Jacobs, G. H. 1989. Color vision in the dog [Aug]. *Vis Neurosci*, 3.119–25.
- Northcutt, R. G. and Kaas, J. H. 1995. The emergence and evolution of mammalian neocortex [Sep]. *Trends Neurosci*, 18.373–9.
- Nowak, M. A., Komarova, N. L. and Niyogi, P. 2001. Evolution of universal grammar [Jan 5]. *Science*, 291.114–8.
- O'Grady, William. 1987. *Principles of Grammar & Learning*. Chicago: University of Chicago Press.
- Ogura, Mieko. 1993. The development of periphrastic *do* in English: A case of lexical diffusion in syntax. *Diachronica*, 10.51–85.
- Ohala, J. J. 1983. Cross-language use of pitch: An ethological view. *Phonetica*, 40.1–18.
- Petrides, Michael. 1991. Functional specialization within the dorsolateral frontal cortex for serial order memory. *Proceedings of the Royal Society of London. B, Biological Sciences*, 246.299–306.
- Pinker, Steven. 1994. *The Language Instinct: How the Mind Creates Language*. New York: Harper Collins Publishers, Inc.
- Pinker, Steven and Bloom, Paul. 1990. Natural language and natural selection. *Behavioral and Brain Sciences*, 13.707–84.
- Premack, Ann James and Premack, David. 1972. Teaching language to an ape. *Scientific American*, 227.92–99.
- Pulvermuller, Friedemann. 2001. Brain reflections of words and their meaning [2001/12/1]. *Trends in Cognitive Sciences*, 5.517–24.
- Reader, S. M. and Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates [Apr 2]. *Proc Natl Acad Sci USA*, 99.4436–41.
- Regier, Terry. 1996. *The Human Semantic Potential: Spatial Language and Constrained Connectionism: Neural Network Modeling and Connectionism*. Cambridge, Massachusetts: MIT Press.
- Ringo, James L. 1991. Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution*, 38.1–6.
- Ross, John Robert. 1979. *Where's English? Individual Differences in Language*

- Ability and Language Behavior*, ed. by Charles J. Fillmore, Daniel Kempler and William S.-Y. Wang, 127–63. New York: Academic Press.
- Sampson, Geoffrey. 1978. Linguistic universals as evidence for empiricism. *Journal of Linguistics*, 14.183–206.
- . 1979. A non-nativist account of language universals. *Linguistics and Philosophy*, 3.99–104.
- . 1980. *Making Sense*. Oxford: Oxford University Press.
- Sarich, Vincent M. 1985. Rodent macromolecular systematics. *Evolutionary Relationships among Rodents*, ed. by W. Patrick Luckett and Jean-Louis Hartenberger, 423–52. New York: Plenum Press.
- Sarich, Vincent M. and Cronin, John E. 1976. Molecular systematics of the Primates. *Molecular Anthropology*, ed. by Morris Goodman and R. E. Tashian, 141–70. New York: Plenum Press.
- Savage-Rumbaugh, E. Sue 1986. *Ape Language From Conditioned Response to Symbol*. New York: Columbia University Press.
- Savage-Rumbaugh, E. Sue and Rumbaugh, Duane M. 1993. The emergence of language. *Tools, Language and Cognition in Human Evolution*, ed. by Kathleen R. Gibson and Tim Ingold, 86–108. Cambridge: Cambridge University Press.
- Savage-Rumbaugh, E. Sue, Murphy, Jeannine, Sevcik, Rose A., Brakke, Karen E., Williams, Shelly L. and Rumbaugh, Duane M. 1993. Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, 58.1–222.
- Sawaguchi, Toshiyuki. 1988. Correlations of cerebral indices for ‘extra’ cortical parts and ecological variables in primates. *Brain, Behavior and Evolution*, 32.129–40.
- . 1990. Relative brain size, stratification, and social structure in Anthropoids. *Primates*, 31.257–72.
- Sawaguchi, Toshiyuki and Kudo, Hiroko. 1990. Neocortical development and social structure in Primates. *Primates*, 31.283–89.
- Schoenemann, P. Thomas. 1997. *An MRI Study of the Relationship Between Human Neuroanatomy and Behavioral Ability*, *Anthropology*, University of California, Berkeley: Unpublished PhD dissertation.
- . 1999. Syntax as an emergent characteristic of the evolution of semantic complexity. *Minds and Machines*, 9.309–46.
- Schoenemann, P. Thomas and Wang, William S.-Y. 1996. Evolutionary principles and the emergence of syntax. *Behavioral and Brain Sciences*, 19.646–47.
- Schusterman, R. J. and Gisinger, R. 1988. Artificial Language comprehension in

- dolphins and sea lions: The essential cognitive skills. *Psychol. Rec.*, 38.311–48.
- Seyfarth, Robert M., Cheney, Dorothy L. and Marler, P. 1980. Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behavior*, 28.1070–94.
- Simon, H. 1962. The architecture of complexity. *Proceedings of the American Philosophical Society*, 106.467–82.
- Smith, B. Holly. 1990. The cost of a large brain. *Behavioral and Brain Sciences*, 13.365–66.
- Snowdon, Charles T. 1990. Language capacities of nonhuman animals. *Yearbook of Physical Anthropology*, 33.215–43.
- Squire, L. R. 1987. *Memory and Brain*. New York: Oxford University Press, Inc.
- Struss, D. T. and Benson, D. F. 1986. *The Frontal Lobes*. New York: Raven Press.
- Tattersall, Ian. 1998. *Becoming Human: Evolution and Human Uniqueness*. New York: Harcourt Brace.
- Traugott, Elizabeth Closs. 1972. *A History of English Syntax*. New York: Holt, Rinehart and Winston.
- Urban, Greg. 2002. Metasignaling and language origins [Mar]. *American Anthropologist*, 104.233–46.
- Van der Loos, H., Welker, E., Dorfl, J. and Rumo, G. 1986. Selective breeding for variations in patterns of mystacial vibrissae of mice. Bilaterally symmetrical strains derived from ICR stock [Mar-Apr]. *J Hered*, 77.66–82.
- Walker, A. and Shipman, P. 1996. *The Wisdom of the Bones: in Search of Human Origins*. New York: Knopf.
- Wang, William S.-Y. 1984. Organum ex machina? *Behavioral and Brain Sciences*, 7.210–11.
- . 1991a. *Explorations in Language*. Taipei, Taiwan: Pyramid Press.
- . 1991b. Explorations in language evolution. *Explorations in Language*, 105–31. Taipei, Taiwan: Pyramid Press.
- Washburn, Sherwood L. 1960. Tools and evolution. *Scientific American*, 203.63–75.
- Watkins, K. E., Dronkers, N. F. and Vargha-Khadem, F. 2002. Behavioural analysis of an inherited speech and language disorder: comparison with acquired aphasia [Mar]. *Brain*, 125.452–64.
- Zuberbuhler, K. 2000a. Referential labelling in Diana monkeys [May]. *Animal Behaviour*, 59.917–27.
- . 2000b. Interspecies semantic communication in two forest primates [Apr

- 7]. *Proceedings of the Royal Society of London. B, Biological Sciences*, 267.713–18.
- . 2001. Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli* [Oct]. *Behavioral Ecology and Sociobiology*, 50.414–22.
- . 2002. A syntactic rule in forest monkey communication [Feb]. *Animal Behaviour*, 63.293–99.