

★ FORUM ★

What Would Lenneberg Think? Biolinguistics in the Third Millennium

W. Tecumseh Fitch

1. Introduction

Biolinguistics, construed broadly as the study of human language from multiple biological viewpoints, was first placed on a solid modern foundation by Eric Lenneberg's impressive *Biological Foundations of Language* in 1967. Lenneberg conceived of our capacity to acquire language as a species-typical aspect of human cognition—a conception so widespread today that it is difficult to realize how radical it seemed to many at the time. Although Lenneberg argued that our language capacity has some species-typical genetic and neural components, he clearly recognized that it has a huge learned, culture-specific component as well. Lenneberg had thus already leap-frogged the unproductive “nature versus nurture” dichotomy that has bedevilled so many debates about language since that time. He also recognized that human language differs in important ways from animal communication, and raised the question of whether the roots of language are best sought in cognition or communication—another prominent preoccupation in modern debates. In short, although he apparently did not adopt the term “biolinguistics” himself, Eric Lenneberg can rightly be seen as an important founding father of contemporary biolinguistics. This makes a celebration in this journal, fifty years later, of his magnum opus highly appropriate.

In this essay, I will first briefly discuss a few of Lenneberg's many insights that I think bear repeating today. Then, I turn to a discussion of modern empirical developments in biolinguistics that I think Lenneberg would find welcome, and in many cases surprising, were he alive today. I will thus focus less on the aspects of Lenneberg's thought that have stood the test of time well, and are still essentially correct today (which covers many of them) and more on aspects where modern data invite a reconsideration of some of his ideas. These come from three general areas: comparative investigations, modern neuroscience and especially molecular genetics. My goal is to provide a concise overview of those developments that I believe, were Lenneberg to appear for a conversation about biolinguistics today, he

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would find most fascinating and in some cases challenging, and to speculate about how he might respond.

2. Lenneberg's Insights

I will first highlight some of Lenneberg's central insights into the biology of language, especially those which appear to have been overlooked in some modern debates. There are many such insights (as well as those where his conceptions, although radical in their time, have become widely accepted), so my selection is personal, and far from comprehensive. I hope that this brief selection inspires contemporary students of biolinguistics to read (or re-read) Lenneberg.

Most crucially, I see Lenneberg's perspective on the biological nature of language acquisition as cutting through some of the most protracted and unproductive debates that continue to rage about language, in particular debates about the roles of genes, environment and culture in language. Lenneberg recognized all of these factors as playing important roles, but did not shy away from highlighting the fact that the human capacity for language is part of human biology and not simply a product of our environment. Starting with the environment, he saw its role as supportive and permissive, but not crucial. In a nice metaphor, he points out that a frog's and a minnow's eggs, developing in the same pond, will reliably yield quite different developmental outcomes (Lenneberg 1967: 373). Of course, the proper nutrients, water, oxygen etc. are needed, but these factors do not determine the outcome: The genetic code and biological aspects of development contained in the eggs at fertilization do. Given this obvious biological fact, why should we be surprised that a human child and a kitten (or a chimpanzee) raised in identical environments should yield different developmental outcomes? The "language-readiness" of the newborn human brain is part of human biology, even if the particular and idiosyncratic end-state reached by any particular individual also obviously incorporates their personal social and environmental history.

Turning to the social and cultural environment, he considered a proper normal social environment to be crucial, but again not instructive in a literal "teaching" sense. Indeed he already was aware that parent's attempts to teach their children specific rules (or to avoid certain words or phrases) are surprisingly ineffective. Acquiring language is not like learning proper etiquette from Miss Manners. Nonetheless, recognizing the centrality of an appropriate linguistic input, he conceptualized the child as "resonating" with this input, rather than memorizing it by rote (see Hoshi, this issue). Cognitively, these led Lenneberg to a conception of "language as a special form of pattern recognition" typical of the human brain, pattern recognition that "can't be accomplished based on probability statistics alone" (Lenneberg 1967: 393).

He explores this idea about resonance in detail, hypothesizing that childhood provides a limited (and again species-specific) period during which the individual is optimally capable of acquiring one or more languages with little effort. This plasticity of childhood is then stabilized at puberty, and the representations formed then undergo consolidation for the rest of an individual's life. Lenneberg can thus be seen as one of the first to recognize the importance of "critical period phenomena" in language acquisition. Today, this is a central and well-accepted concept in

child language acquisition, although the more nuanced modern conception, often termed “sensitive periods,” acknowledges the more gradual “closing” of the period than the slamming shut at puberty portrayed by Lenneberg. And, again taking an essentially modern biological viewpoint, he recognizes that there is nothing surprising or special about such critical periods: We find them everywhere in biology, from bird imprinting to cat visual development, and human sensitive periods are just one more example.

Also impressive is Lenneberg’s conception of the potential nature of “universal” properties of human languages. He clearly recognizes that these must be abstract properties that depend on the universality of the cognitive mechanisms underlying language, and not either the categories or operations seen more superficially in particular languages. It is thus ironic that several recent critiques of the notion of language universals and “universal grammar” have unabashedly taken on the latter rather than the former (e.g., Everett 2005, Tomasello 2005, Evans & Levinson 2009). These critics seek, and then reject the existence of, superficial commonalities, rather than considering the deeper cognitive commonalities that Lenneberg and Chomsky, at around the same time (Chomsky 1965), had in mind when discussing “universal grammar”. Contemporary critics also often neglect the kind of statistical or implicational universals, discussed extensively at around the same time by Greenberg and many others (Greenberg 1963, Greenberg, Osgood & Jenkins 1966). This is an example of the dictum that those who fail to learn from history are doomed to repeat it (cf. Fitch 2011).

Finally, Lenneberg weighs in on two central topics in modern debates concerning language evolution. First, considering arguments about the relative importance of peripheral anatomy vs. central cognition in the capacity for language, he comes down clearly on the central side: Neurophysiological factors are central (Lenneberg 1967: 57). But, Lenneberg argues, these central factors are not simply a product of brain size, given that nanocephalic dwarves with brains within the ape size range can possess normal language. The implication is that we cannot use cranial capacity, or other measures obtainable from the fossil record, as an indication of when language arose, or clues as to what its earlier form(s) might have been (cf. Fitch 2009).

Second, in chapter 8 Lenneberg considers and rejects arguments about linguistic relativity made by Benjamin Whorf and others. Although many superficial differences between languages exist in vocabulary, grammatical categories, and many other factors, and these may effect communication, they do not change the central capacity for conceptualization. He concludes that language depends on cognition much more than cognition depends on language.

As mentioned, this is just a taste of the many insights Lenneberg presents in his book. Some of these insights (e.g. regarding critical periods, or the idea that the language-ready brain is part of human biology) have been widely accepted today, at least among academics in the relevant disciplines. Others (e.g. concerning the nature of language universals, or the centrality of cognitive factors) are still debated and/or remain inadequately appreciated by some, even fifty years later. But in my opinion, in all of these cases, Lenneberg was clearly on the right track.

3. How far Have We Come? Biolinguistics Today

Above I highlighted areas where Lenneberg would be either pleased to see his ideas accepted or alternately would roll his eyes at how issues and dichotomies he had already cogently resolved continue to be debated today. I now turn to three areas where I think Lenneberg would be pleasantly surprised at the progress we have made in researching the biological foundations of language. These are comparative biology and animal cognition in particular, neuroscience (especially brain imaging), and molecular genetics. In all of these areas, I think, Lenneberg would be astounded by how much science has progressed, sometimes in ways consistent with his arguments and predictions and sometimes less so.

3.1. *Comparative Cognition Research*

Although Lenneberg considered animal cognition and communication research briefly, his main concern was distinguishing between these and their human analogs. He, rightly in my opinion, drew a sharp distinction between animal communication systems known at that time and human language; this was one part of his argument as to the primacy of cognitive factors rather than communicative factors in the biology of language. In a detailed discussion of word meanings, he pointed out (again rightly) that human word meanings are nothing like stimulus-response reactions to particular things. Rather, words reflect concepts and categories, often in a very flexible and context-dependent manner (also see Leivada, this issue). Lenneberg argued that words thus “represent” in a very different way from the calls of animal communication systems. He cited two examples of this (Lenneberg 1967: 329–330): A dog trained to “point” at a tree or door in his masters yard is unable to locate and point to the equivalent referents in a neighbor’s yard; and a parrot trained to say “goodbye” when people leave the room sometimes do so when people enter as well. In neither case were any references given, so we must assume these are anecdotal reports.

Modern research has elaborated upon these ideas, using well-controlled experimental investigations, in three ways. The first, and perhaps most widely known, was the discovery that some monkeys do produce alarm calls that have rather general apparent referents. For example, vervet monkeys produce three different alarm call types when seeing different predators: large aerial predators like eagles, dangerous land predators like leopards, and less-dangerous large snakes (Struhsaker 1967). Experimental investigations of these calls using playback experiments demonstrated that listening vervets interpret these calls as if they had spotted the relevant predator type themselves (Seyfarth & Cheney 1980, Seyfarth, Cheney & Marler 1980, Seyfarth & Cheney 1984). We now know that such predator-specific alarm calls have evolved, convergently, in many different bird and mammal species, including chickens, ground squirrels, meerkats, and various other monkey species (Sherman 1985, Macedonia 1991, Evans, Evans & Marler 1993, Zuberbühler 2001, Manser, Seyfarth & Cheney 2002, Zuberbühler 2003).

Are these the equivalent of “animal words”? There are several good reasons to think not. Early authors were careful to label these calls “functionally referential” to indicate that they can be parsed by listeners as evidence about predators, but this does not entail that signalers intend to communicate the predator’s pres-

ence to ignorant receivers (Cheney & Seyfarth 1990). Indeed abundant subsequent work suggests that the latter is not the case, and that indeed monkeys lack a rich enough “theory of mind” to actively represent the ignorance of their conspecifics that would be required to hold such an intention (Seyfarth & Cheney 2003, Cheney & Seyfarth 2007). Thus, it is perfectly possible that, from a signaler’s point of view, a particular call mainly reflects arousal caused by sighting a predator, but for the perceiver this functions as an indication of that predator’s presence (cf. Wheeler & Fischer 2012, Fitch & Zuberbühler 2013). From a modern perspective then, this particular glass is half-full: it points to a phylogenetic continuity in perceivers (sophisticated, inferential, context-dependent interpretation) but a remaining discontinuity in terms of signalers (Seyfarth & Cheney 2014, 2016). Lenneberg would be fascinated by all this, but point out that the distinction between linguistic meanings in language and “semantics” of these alarm call remains clear.

Regarding dogs’ ability to interpret meanings, this issue has now been investigated experimentally in several dogs with extraordinarily large vocabularies including more than 100 object referents (Kaminski, Call & Fischer 2004, Pilley & Reid 2011, Griebel & Oller 2012). Two facets of these data are relevant. First, the border collie “Rico” showed evidence of fast mapping (one trial learning of a word meaning) and long-term retention of that meaning, although the strength of this experimental demonstration has been questioned based on results from another dog (Kaminski, Call & Fischer 2004, Griebel & Oller 2012). Second, another border collie “Chaser” successfully mastered over 1000 object referents, and unlike Rico (who simply retrieved named unique objects) could also produce specific transitive actions to these objects, differentiating the three sentences “nose ball”, “paw ball”, and “bring ball”. Chaser could also use names to refer to categories like “toy” or “ball” that applied to many different objects (Expt. 3, Pilley & Reid 2011). This both shows that dogs are not limited to learning specific object-word pairs, as Lenneberg had claimed, but also have a productive ability to map from utterances to action-object pairings. Lenneberg argues that proper names are in some sense a degenerate form of word meaning (given their typical pairing with specific individuals), and these dog experiments pair specific words with specific objects, and could thus also be seen as degenerate “proper names”. But the understanding of novel object/action pairings documented for Chaser belie Lenneberg’s argument that the productive, creative ability to understand novel combinations is unique to humans.

Finally, and for me most convincingly, the results from language-trained African gray parrots experimentally demonstrate both flexible, context-dependent interpretation of meaning (including adjectives like shape, color, material, and number) and appropriate productive usage of these abstract categories (Pepperberg 1981, Pepperberg & Brezinsky 1991, Pepperberg 1999). Although many parrots learn to imitate speech, the meaningful comprehension and use of words requires special training (the model-rival paradigm), and few parrots have successfully undergone this intensive procedure, which more closely resembles child language acquisition than more typical training procedures (Pepperberg 1985). Although in the parrot case both vocal imitation and its meaningful deployment are clearly the result of convergent evolution, they nonetheless belie Lenneberg’s arguments about human-typical usage of meaning being unique to our species: Important components of this are found in multiple other species.

What would Lenneberg's reaction to these data be? First, he would correctly point out that in all of these cases, it appears that the "semantic" behaviors exhibited by non-human animals evolved convergently relative to our own. Even regarding nonhuman primates, we have no evidence for predator-specific alarm calls in great apes, so the presence of such calls in some monkeys is not evidence that they were present in our common ancestor with these monkeys. Nonetheless, these data clearly show that Lenneberg's claims of "unique to man" are incorrect. More importantly, although Lenneberg recognized that repeated convergent evolution can provide evidence about adaptive function (Chapters 1 and 9), he does not seem to recognize that such analogies are also relevant to testing mechanistic hypotheses, for example hypotheses regarding the brain mechanisms needed to perform these feats (for dogs see e.g. Andics et al. 2014, Andics et al. 2016). Although only homology can be used to infer phylogenetic trajectories, as Lenneberg realized, this does not make analogy irrelevant (cf. Fitch 2010, 2017).

I think that these modern data steals the wind from the sails of Lenneberg's critique of Otto Koehler, with whom Lenneberg only partially agreed (1967: 232). In fact, Koehler was one of the first to persuasively argue for a multi-component perspective on the biology of language (Koehler 1951, 1954). Today, a multi-component approach to biolinguistics, including animal cognition as a key ingredient, is widely seen as the most promising comparative framework within which to consider the evolution of language (Hauser, Chomsky & Fitch 2002, Fitch, Hauser & Chomsky 2005, Fitch 2017); I suspect that given today's data Lenneberg would concur.

3.2. *Neuroscience and Brain Imaging*

I think that modern progress in neuroscientific methodology would have pleased (and astounded) Lenneberg. In his day, essentially the only neural data relevant to language came from either clinical anomalies (like the genetic dwarfism that he highlighted) or patients suffering from brain lesions. In the latter case, there were no methods like computed tomography (CT) scans or magnetic resonance imaging (MRI) to probe brain anatomy in living individuals, so investigation relied either on clinical signs (e.g. hemiparesis) or post-mortem dissection. Thus, the degree to which Lenneberg could interpret data from his observations of living patients in terms of lesion location was extremely limited. Indeed he is somewhat dismissive of the relevance of localized lesions. Although he worked with Norman Geschwind's patients (Lenneberg 1967: 196), he mentions Geschwind's then new but now classic 1965 paper, defending the importance of the arcuate fasciculus in connecting frontal and temporal regions, only in passing as "an opposite point of view" (Lenneberg 1967: 217), without further discussion. In a book which leaves few stones unturned, this is a surprising dismissal.

Since the 1970s and the introduction of CT scans, and then later MRI, neurologists have benefited from a much richer and more accurate means of determining lesion location and of linking it to a patient's symptoms. The result has been a revival, with modifications, of the older models of Broca, Wernicke, and Lichtheim which attempted to localize particular sub-components of language (such as producing vs. understanding speech, or processing syntax) to particular brain regions (Geschwind 1970, Caramazza & Zurif 1976, Damasio & Geschwind

1984, Damasio & Damasio 1992). The later introduction of positron emission tomography (PET) and functional MRI (fMRI), which allowed measurement of brain activity in living patients, further amplified this localizationist trend. Although sometimes veering into “neo-phrenology” (cf. Blumstein 1979, Friston 2002), there can be little doubt that these modern brain imaging methods have provided a massive new source of relevant data, and have strongly influenced contemporary neuro-linguistics. Lenneberg would be amazed.

Lenneberg might have been less impressed with the various theoretical edifices which have been built up around this new font of neurolinguistic data, because some make little contact with findings from linguistics, and even those that do often adopt radically different theoretical approaches (compare, for example, Ullman 2001, Hagoort 2005, Price 2010, Friederici 2011, Rogalsky & Hickok 2011). Given that Lenneberg’s book ends with an appendix by Noam Chomsky detailing formal considerations for evaluating computational approaches to language, Lenneberg might be disappointed to see how rarely formal and computational linguistic considerations play a role in current discussions of the neural basis of language.

To briefly consider a neurolinguistic approach that does take formal and computational considerations seriously, consider the recent brain imaging work of Angela Friederici and colleagues (Bahlmann, Schubotz & Friederici 2008, Bahlmann et al. 2009, Friederici 2011, 2012, 2017). Starting with two well-defined artificial grammars (a finite-state and context-free grammar), these researchers first found that different frontal regions were activated in participants trained to process the two grammars (Friederici et al. 2006). Furthermore, these two regions were connected to the temporal cortex by very different white matter tracts: the frontal operculum (activated by the simpler grammar) was mainly connected via a ventral pathway, while the portion of Broca’s area activated by the context-free grammar (Brodmann area [BA] 44) was connected by a dorsal pathway roughly equivalent to Geschwind’s arcuate fasciculus (Friederici et al. 2006). Later experiments showed the same region activated by a strictly hierarchical, center-embedded grammar, suggesting that this activation is not due to any simpler strategy, like counting, being adopted to process the context-free grammar (Bahlmann, Schubotz & Friederici 2008), and that the same region is increasingly activated by increasingly complex syntactic constructions in German (Makuuchi et al. 2009).

The conclusion that portions of Broca’s region play a key role in processing syntax, whether in natural language or in various more artificial tasks, was verified in a meta-analysis (Friederici 2011) as well as numerous experiments in other laboratories (Pallier, Devauchelle & Dehaene 2011, Uddén & Bahlmann 2012, Hagoort 2014, Dehaene et al. 2015). It remains unclear to what degree this rather broad region is specifically involved in linguistic syntax (as opposed to, say, musical syntax), but that at least portions play a key role in processing language appears indubitable (Koelsch et al. 2002, Fazio et al. 2009, Fedorenko, Duncan & Kanwisher 2013, Fitch & Martins 2014). For a dissenting view, see Rogalsky & Hickok (2011).

This brain imaging research also makes a fascinating connection to neuro-anatomical work in nonhuman primates. Direct cytoarchitectonically guided comparisons between Broca’s region in human and chimpanzee post-mortem brains shows that this area is the most enlarged cortical region known in the human brain, with left BA 45 six times and left BA 44 6.6 times larger in humans than in chim-

panzees (Schenker et al. 2010). Although the entire human brain is three times larger than a chimpanzee's, primary sensory regions are not greatly enlarged: primary visual cortex is only 1.8 times larger in humans than chimpanzees (Schenker et al. 2010). Furthermore, these areas are much more heavily connected, via a dorsal pathway, to a much wider swathe of parietal and temporal cortex in humans (Rilling et al. 2008).

This combination of comparative and neuroimaging data have led me to suggest that Broca's region plays the computational role of a "stack", a form of auxiliary memory required for processing of grammars above the finite-state or "regular" level (Fitch 2014). According to this "dendrophilia hypothesis" (Fitch 2014), the enlargement of Broca's region greatly expanded the capacity of this auxiliary memory, and its drastically increased connectivity increased its ability to serve multiple functions for multiple brain regions (rather than being limited to a single modality or cognitive domain). I believe that, whether this hypothesis turns out to be correct in its details or not, it is the kind of hypothesis Lenneberg would favor if he were alive today, given his emphasis on a broad range of biological data consistent with linguistic theory.

Two other neurolinguistic issues raised by Lenneberg deserve emphasis. One is his emphasis, typical at that time, on the importance of cerebral asymmetry in human language, and in particular the left hemisphere bias observed in some aspects of language processing. This degree of left bias was thought by many at the time to be unique to humans. For example:

The phenomenon of cerebral dominance—that is, the predominant importance of one side of the brain for a class of learned behavior—occurs, as far as we know, in no mammal other than man.

(Geschwind 1970: 944)

Geschwind was careful to say "in no mammal" because it was already known from the work of Fernando Nottebohm that song control in some birds was left-lateralized (Nottebohm 1971). In any case, it is now clear that cerebral asymmetry is found, and indeed appears to be typical, in a wide variety of vertebrates including fish, birds and mammals (Bisazza, Rogers & Vallortigara 1998, Vallortigara 2000, Rogers & Andrew 2002). To the extent that aspects of human language are lateralized, they are not unique or even unusual in this respect, compared to perceptual processes in vertebrates in general, or primates in particular (cf. Fitch & Braccini 2013).

In contrast, an observation emphasized by Lenneberg that seems to have held up today concerns the significance of absolute brain size for linguistic ability. Citing the clinical work of Seckel on nanocephalic dwarfism (Seckel 1960), in which humans have very small brains in the range of chimpanzees but nonetheless have preserved linguistic abilities, Lenneberg suggested that the "absolute increase in cell number and axodendritic density have increased man's psychological storage capacity" (Lenneberg 1967: 69) and other more general cognitive abilities, but not our capacity for language. Although nanocephalic dwarves suffer general cognitive deficits, they nonetheless acquire the rudiments of speaking and understanding, and most master verbal skills to at least the level of five-year-old children. Lenneberg concluded, correctly I think, that "the organization of the brain is more

important for language than its mass" (Lenneberg 1967: 70). This conclusion is consistent with most current thinking in neurolinguistics.

3.3. *Molecular Genetics, Deep Homology and Paleo-DNA*

I turn finally to a source of data that would probably have most astounded Lenneberg: the accurate sequencing of DNA recovered from long-extinct hominins like Neanderthals and Denisovans (Green et al. 2010, Meyer et al. 2012). The general progress made in genetics since Lenneberg's time (genetic engineering, optogenetics, personal genome sequencing, etc.) is by itself astonishing, and continues to accelerate. But the notion that we would be able to recover DNA from an extinct species in enough detail to begin reconstructing its phenotype seemed fanciful even in 2000, after the first sequence data of the mitochondrial DNA from a Neanderthal was reported (Krings et al. 1997). The reason is that each cell contains many mitochondria (typically hundreds or thousands per cell), each of which has multiple copies of the whole genome, meaning that there are typically thousands copies of the mitochondrial DNA for each copy of nuclear DNA. The mitochondrial genome is also much shorter than the nuclear genome, and is arranged on a circular chromosome yielding greater stability. It is thus easier to piece together from the very short sequences typically recovered from ancient DNA. For these reasons it initially seemed likely mitochondrial DNA would be all we could ever extract and sequence from fossils: useful but very far from complete.

But ten years afterward, due to improved sample quality, sequencing technology, and computational tools, the unimaginable became true and sequence data covering much of the Neanderthal genome was reported (Green et al. 2010), with the bombshell finding that a small amount of interbreeding had occurred between Neanderthals and modern humans (cf. Pääbo 2014). A few years later, a high quality full-coverage genome was released (Prüfer et al. 2014), which allowed a short list of 87 genes with protein-coding differences between Neanderthals and ourselves to be drawn up (see supplementary online material for Prüfer et al. 2014).

To the extent that we can interpret these genetic differences and similarities, the Neanderthal genome offers an unparalleled opportunity to test hypotheses about the existence of particular components of language in this extinct species, and thus to derive inferences about the "protolanguage" that might have characterized this species (cf. Fitch 2017). Our problem at present is that few genetic variants have been isolated that can be definitively linked to any particular component of language. However, one such example does exist already: the human-specific form of the *FOXP2* gene. This gene was first identified due to its mutation in a British family, some of whose members suffer from developmental dyspraxia specific to oro-motor control, which leads to a severe developmental speech disorder despite otherwise relatively spared cognitive and linguistic abilities (Vargha-Khadem et al. 1998, Vargha-Khadem et al. 2005). Since this discovery, multiple other individuals with *FOXP2* mutations and a similar phenotype have been discovered (Pääbo 2014, Graham & Fisher 2015).

The *FOXP2* gene codes for a transcription factor (a protein that can bind to DNA and thus modify the expression of other genes) connected with a rather large network of associated genes that can be up- or down-regulated (Vernes et al. 2007).

Crucially, in all modern humans, *FOXP2* exists in a human-specific allele, coding a protein that differs from that of chimpanzees (Enard et al. 2002). Within-species homogeneity is just what we should expect for a gene causally associated with language evolution (since humans around the world have the same capacity to acquire any language), as is a difference from chimpanzees (which lack this capacity). Thus *FOXP2* has the appropriate characteristics required of a language-evolution-related gene, albeit one that is tied to speech output capabilities rather than more central linguistic characteristics like syntax.

Crucially, once the Neanderthal genome was sequenced, it was possible to evaluate the sequence of *FOXP2* in this species as well, and the Neanderthal gene turned out to code for the same derived protein as in modern humans (Krause et al. 2007). This strongly suggests that the selective event that led this derived variant to be selected in our hominin ancestors preceded our divergence from Neanderthals, a split which occurred roughly 500,000 years ago. Although it is important to note that no single gene alone underlies the derived human capability for speech, this finding in turn suggests that selection for improved oro-motor sequencing also preceded this split, suggesting that increased oro-motor sequencing abilities characterized our common ancestor with Neanderthals (cf. Fitch 2017). This is obviously consistent with the hypothesis that this common ancestor had already acquired the capacity for speech. Finally, because the paleontological record strongly suggests that Neanderthals did not have fully modern cognition (Tattersall 2016), this suggests that this common ancestor, like Neanderthals, lacked some other crucial component of language (e.g., hierarchical syntax or theory of mind, cf. Bolhuis et al. 2014). Although no single gene by itself can explain language, or even key sub-components of language like oro-motor sequencing or dendrophilia, this case of *FOXP2* provides a promissory note for future, similar genetic investigations, rather than a complete story in itself.

Of course, the complexity of the mapping between genes, development, and cognitive abilities is highly indirect and complex (DeSalle & Tattersall 2017, Fisher 2017), and we should not let the excitement about *FOXP2* above obscure the fact that most of the known genes associated with language and language disorders have less clear and striking phenotypic effects. Any single gene acts in a context provided by other genes, and its effects often vary from tissue to tissue, and probably differ in different brain regions. It is also important to note that many genetic changes relevant to evolution result in changes in gene regulation during development rather than protein-coding changes in the gene product. Indeed, outside of the protein-coding portion of the *FOXP2* gene, a modification of a putative regulatory region has been discovered which is not shared with Neanderthals (Maricic et al. 2013), suggesting that there may have been waves of selection on this gene, and the most recent one is unique to *Homo sapiens*. We have a long way to go before even this single gene is understood, much less the multiple changes in many genes, related to multiple different mechanisms, that must have accompanied the evolution of language.

Nonetheless, this new source of paleo-genetic data clearly refutes the all-too-common notion that “we will never know” what happened when during hominin evolution, and opens the prospect of testing competing models of language evolution empirically. Lenneberg would be amazed.

Although many other genes besides *FOXP2* have been proposed to be associated with human language abilities (Graham & Fisher 2015, Mozzi et al. 2016), none of these candidates yet has both the clear phenotypic identification and the pattern of within-human homogeneity and human/chimpanzee differences that would be required to firmly identify it as a language-related gene. Fortunately, however, the process of identifying and isolating gene variants in individuals is now part of normal clinical genetic practice and individualized genomics, so we can confidently await more examples in the coming years. For each of these candidate genes, we can immediately cross-reference with the Neanderthal genome (and paleo-genomes from other extinct hominins) to see if they shared the modern human allele or not, and build a clearer and clearer picture of what the (already known) genetic differences between us, Neanderthals, and chimpanzees actually mean for development and the human phenotype. Thus, in my opinion, the most promising data-driven pathway for examining the linguistic (and other cognitive) abilities of Neanderthals and other extinct hominins is by examining their DNA.

4. Conclusion

In this paper I have attempted to revisit some of the key notions discussed by Lenneberg in his ground-breaking book from a modern, empirical perspective. Although, in many ways, Lenneberg was on the right track, and new sources of data have simply reinforced points he made fifty years ago, in others his conclusions have been updated, challenged or even rejected. In sum, however, I think it is fair to say that the broad, data-driven approach that he pioneered, firmly based in both the biology and linguistics of his time, has aged well. There is still much to be found in his book that remains of value for biolinguists today.

In addition, I tried in the second part of this essay to show how far the field of biolinguistics has come since Lenneberg's time, building on a set of questions he was one of the first to cogently ask, and within a framework he laid out beautifully in the late 1960s. I believe that, were he alive today, Lenneberg would be pleased by this progress, and excited by the prospects for the future.

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W. Tecumseh Fitch
University of Vienna
Department of Cognitive Biology
Althanstrasse 14
1090 Vienna
Austria
tecumseh.fitch@univie.ac.at