Draft chapter for *Embodiment in Evolution and Culture.* T. Fuchs & C. Tewes, eds. (2016), pp. 129-149

On Human (Symbolic) Nature:
How the Word Became Flesh

Terrence W. Deacon

Abstract: The concept of human nature has been challenged by social scientists because of its inability to clearly delineate the distinction between the biologically inherited and experientially acquired attributes of being human. Yet the very fact of being susceptible to acquired cultural influences irrelevant to other species makes clear that this is an evolutionarily constrained susceptibility. Symbolic processes are the source of the most important and distinctively human acquired influences, and include both linguistically mediated and habitually reproduced social conventions. Susceptibility to these influences arose due to the evolution of neurological adaptations that support symbolic communication and cognition. Although human brains do not include any structures that lack ape homologues, the slight reorganization that made symbolic abilities ubiquitous has also created the possibility for socially transmitted information to radically reorganize mental functions. In this essay I re-analyze the concept of symbolic reference in order to overcome equivocal and ambiguous uses of the concept that obscure the special nature of these adaptations and thus blind research to the complex bio-cultural interactions that produce some of the most ubiquitous and unprecedented features of being human. These include modifications of memory functions, emotional experiences, the nature of identity, and the range of mental plasticity.

Introduction

Humans are a member of the family of African apes that also includes gorillas, chimpanzees, and bonobos. And yet this phylogenetic characterization of our species provides a very misleading characterization of what is shared with our ape cousins and what makes us distinct – in other words, what has traditionally been called human nature. The concept of human nature has a long and troubled history (Bock 1980, Hull 1986). Most often it has been used to designate some putative set of universally shared biologically inherited psychological traits constituting the so-called "psychic unity" of humankind (the term "psychic" is used here and below in its traditional non-mystical sense). As an essentialist enterprise, the effort to enumerate this set has failed (Ingold 2006). This turned out to be futile for the same reason that identifying the set of physiognomic traits that are shared by all and only members of the same species fails to unambiguously define a species.

Today, in the era of gene sequencing, taxonomists ground their determination of biological group membership on common genetic ancestry. Thus, as the opening statement of this essay indicates, we humans derive our genetic inheritance from the common ancestor of all African apes. Indeed, using genetic criteria it is possible to trace our ancestry all the way back to the so-called last universal common ancestor (LUCA) of all life on earth, grouping us with ever-larger more inclusive clades. The new rule of thumb for analyzing biological ancestry could thus be characterized as “follow the (genetic) information.” Membership within a phylogenetic group – whether species or kingdom – is ultimately determined by all members sharing genetic continuity through a common ancestor.

But this cladistic approach, if pursued exhaustively, can lead to a problematic result even just in terms of phylogenetic genealogy. This is because organisms include large amounts of genetic material that gets shuffled and recombined during evolution, and in some case can involve highly distinct inheritance pathways. For example, the lateral transfer of genetic material between bacteria makes simple genealogical determination of the equivalent of a bacterial species essentially impossible. But even eukaryotic organisms such as ourselves, have dual ancestry. Though this is not the result of lateral gene transfer or because we have two parents. It is because the genealogies of our nuclear and mitochondrial genomes are quite radically separate. Our nuclear genes place us in a lineage that traces back to primitive single cell Archaea, whereas our mitochondria have a separate genome that shows them to be members of the Bacteria. These genetic lineages evolved in parallel and with respect to one another due to the endosymbiosis of a bacterial lineage within an archaean cell lineage well over a billion years ago. In the subsequent epoch of eukaryotic evolution, each genome has undergone radical reorganization in functional interaction with the other. As a result, there has been a sort of informational, though not molecular, lateral influence of the one on the other.

In many respects we humans also have dual psychic ancestry. One lineage is continuous with our African ape cousins, tracing back from there to all primates, mammals, terrestrial vertebrates, and so on. I will describe it as our primate mental genealogy, though many features antedate the origin of the primate clade. The other lineage is not traceable through molecular genetics, but through continuous social transmission. I will describe this as our symbolic genealogy.

This dual inheritance perspective is not new. And in many respects it remains quite controversial to describe it in terms of parallel evolutionary processes. But the relationship I am describing should not be confused with dual inheritance theories that dichotomize genetic and social transmission processes, as this is defined in so called bio-social evolution theories. In many respects my point is the opposite. It is their inextricable entanglement that I want to emphasize.

The interactions between biological and social information transmission is not what distinguishes these two cognitive-behavioral genealogies. The significant roles of epigenetic and niche-borne sources of inherited biases and constraints on the development of behavior and cognition are now well established. This undermines simple innate / learned, nature / nurture conceptions of behavioral evolution in social species in general, not just in humans. The transmission of cognitive, behavioral, and social predispositions down the primate-human lineage necessarily involved both social continuity and genetic continuity. So it is not the difference between molecular genetic and social transmission that I am interested in highlighting, but rather the entanglement of the symbolic component of social inheritance with non-symbolic social-cognitive inheritance, and how this interaction has influenced the evolution of their genetically and epigenetically mediated biological supports.

This brings up another parallel with the evolution of eukaryotic cells that should be mentioned before proceeding. The coupling of previously autonomous organisms which ultimately gave rise to mitochondrial and nuclear genomes did not merely constitute a cooperative relationship. It gave rise to an unprecedented new level of biological unity, and with it unprecedented new modes of evolution. The genetic information that characterized each of these once independent lineages has been fundamentally changed by their fusion and co-dependence. Each has been degraded and modified by the ubiquitous presence of the other over more than a billion years to the point that they are no longer even separable informational lineages.

Unlike the two lineages that came together to give rise to eukaryotic organisms, however, our primate and symbolic psychic lineages had unrelated origins and originated in epochs separated by tens of millions of years. The many overlapping cognitive, sensory-motor, and social-emotional predispositions that monkeys and apes inherited from the common ancestral anthropoid primate arose within the last 60 million years. In contrast the unbroken lineage of symbolic information almost certainly doesn't extend back more than about 2.5 million years, and may have a far more recent origin. The radical incommensurability of these yoked semiotic genealogies is what makes human nature so difficult to characterize in typical biological terms, and also dooms any effort to partition humanness into inherited and acquired (e. g., nature versus nurture) components. It is an unprecedented entanglement of genealogies that comprises a highly distinctive universally shared nature that sets us apart from all other species on earth.

Like the separate but interdependent genetics of mitochondrial and nuclear DNA, our symbolic genealogy has significantly influenced the evolution of our primate psychic genealogy, and vice versa. Like the fused genetic lineages that became eukaryotic information, these two psychic lineages that became entangled during our distinctive ancestry are no longer separable. Each has been fundamentally transformed by the other over this shared evolutionary history so that our biology can't be understood apart from the symbolic cultural context that it is informed by. This is why in my 1997 book (Deacon 1997) I described humans as a "symbolic species," analogous to the way we might characterize birds as aerial species and dolphins as aquatic species. But unlike these ecologically specialized lineages, the symbolic "ecology" that humans evolved to fit is not external to the human lineage. It is inextricably part of it.

1. Symbols Oversimplified

In my view one of the most serious impediments to understanding what is distinct about human cognition is a fundamental misunderstanding about the nature of symbolic reference. As a result, our ability to understand the influence of our symbolic genealogy is severely compromised. This difficulty needs to be cleared up before we can hope to make sense of the common essence that defines humanness.

Ironically, the symbol concept has been the victim of oversimplification by linguistic theory itself. Language is the very phenomenon most in need of explanation and yet its unprecedented mode of referring is often treated as though it is self-evident. According to this common conception of linguistic symbolization it is merely an arbitrary (unconstrained) mapping relation between two classes of objects – signifiers and what they signify – linked only by convention. From this perspective, linguistic reference appears as simple as possible, involving minimal defining criteria compared to other forms of reference. In comparison, iconic signs require some formal correspondence with what they signify and indexical signs require some factual connection with what they signify.

Conceived in these terms, symbolic reference is often defined negatively; simply as reference that does not depend on either criterion; thus arbitrary. It would seem, then, that symbolic reference is primary and both iconic and indexical reference forms are the more complex and derived forms.

But this superficial characterization is deeply flawed. Bracketed from this analysis is any consideration of how these relations are interpreted and how they could have become established. Much of this is cryptically supplied by an unanalyzed concept of convention. Most uses of the term assume that it refers to formally or tacitly agreed-upon rules or habits of behavior or patterns of use in some domain of social interaction. Its basis has become a topic of considerable philosophical debate with such philosophical luminaries as Quine, Davidson, Lewis, and Millikan (to name just a few) presenting conflicting accounts. However, what is common to all is the recognition that the establishment of conventions occurs in a context of end-directed interaction among agents that each interpret the behaviors of the others as significant in some respect. In other words, conventions result from complex semiotic processes that are not at all arbitrary.

Though the problem doesn't begin with Ferdinand de Saussure's theory of language, the influence of this theory has perpetuated the problem. The concept of arbitrarity pertains to the relationship between sign vehicle attributes and the attributes of what it signifies. The problem arises from a synchronic (a.k.a. structuralist) account of how words refer. Only paying attention to the obvious fact that word sounds do not mimic or resemble what they refer to, their linkage to what they are about seems merely arbitrary. Moreover, signifiers (as Saussure termed the sign vehicles of language, e. g., words) are treated as the most basic types of signs by virtue of being defined by lacking properties shared with what they signify.

Contrasting this with sign forms that share properties with what they signify, symbolic forms thereby appear arbitrary and simple. A bit of careful reflection, however, demonstrates that it is not sign vehicle attributes that determine whether reference is being mediated by iconic, indexical, or symbolic means.

Arbitrariness is a negative way of defining symbols. It basically tells us that neither formal likeness nor factual correlation are used as the basis for symbolic reference. But this is inadequate. It fails to specify exactly how the symbolic referential relation is established. So, even though this is a common shorthand way of characterizing symbolic reference it merely passes the buck, so to speak, to some assumed and undescribed means by which reference is established. In fact, all semiotic relationships include some degree of arbitrarity, because those attributes that are taken as the ground for the sign-object linkage can be chosen from many dimensions, and only some will be utilized (if any). What matters, then, is the interpretive process and how it makes use of sign vehicle attributes and the attributes of what is intended as a referent.

In this respect, we can say that anything can be chosen as a sign vehicle to represent anything else and by any mode, depending on the interpretive process involved. For example, depending on the interpreter and social context the same facial grimace can be interpreted as a sign of pain, a neurological disorder, or the communication of social censure. Or the sight of smoke can be seen to resemble a cloud, to indicate a fire, or to signal the election of a pope. The relevant property is selected by the interpreter and what is being referred to depends on the capacity of the interpreter to use that property in a particular way.

So, turning this initial logic of semiotic categorization on its head we can ask: What constitutes the interpretive capacity to comprehend a given referential relationship as either iconic, indexical, or symbolic? In the case of iconic and indexical relationships the sign vehicle itself includes properties that provide some evidence as to its relation to what it refers to. But where there is no interpretive support given by any sign vehicle property, all the interpretive clues must be supplied by the interpreter. This is, of course, made obvious when a traveler is confronted with an unfamiliar language or when an archaeologist comes upon a stone tablet inscribed with an unknown form of writing. Without some external source of information, some non-arbitrary semiotic basis, the meaning is effectively encrypted. In contrast, even though we know nothing of the beliefs and rituals of the stone-age people who painted on cave walls in Southern France, we immediately recognize the idealized forms of animals and humans painted by these stone-age "artists." Interpreting their iconic content is almost trivial, while interpreting their symbolic significance is forever beyond our reach. In order to be able to interpret the symbolic meaning of cave paintings or the words of an ancient lost language one would need some prior experience with the patterns and habits of use of these symbolic artifacts within a cultural network of other icons, indices, and symbols. In other words, this requires acquaintance with the semiotic conventions in which the symbols are embedded.

Similarly, children acquire their facility with language as its symbols are embedded in activities of pointing, soliciting shared attention, playful and instrumental interactions, observing the complex correspondences between symbols, objects, and events in social activities, etc. All of these activities are constituted by non-symbolic forms of communication and interpretation. Only in this way can the apparent arbitrarity of symbolic reference be grounded in communications and actions that are not arbitrary.

So by simply equating symbolic reference with arbitrary correspondence its complex infrastructure and historical grounding is ignored. In addition, the simplified assumption that the nature of convention is just a correspondence relationship glosses over another critical distinction. This is the distinction between properties that distinguish types of sign vehicles and properties that determine how a sign vehicle refers to something that it is not. Both relations involve conventionality, but in different and partially independent ways. Symbols are in this respect doubly conventional. They are conventionally derived sign vehicles that refer to things via conventionally determined means.

As the father of semiotic theory Charles Peirce pointed out over a century ago, we must distinguish properties of a sign vehicle (e. g., a drawing or spoken word), from properties taken to link it to its object of reference. So a conventional sign vehicle can serve as the basis for iconic and indexical reference, as well as symbolic. There can be conventionalized typographical icons (e. g., the typographical smiley face).

Iconic reference depends on shared formal properties between the sign vehicle and what it refers to. For example, with a bit of imagination a face can be discerned on the full moon, or in a cloud formation, and it might even remind you of someone you know. But iconism can also be highly abstract. A mathematical equation refers iconically, once you know how to discern its symbol-mediated isometry (e. g., between the structure of the interpreted equation and a corresponding geometric or dynamical relationship). An equation can be interpreted to be iconic (e. g., of a parabolic trajectory) only, however, if you know how to discern the way that differences in the mathematical values or operations directly correspond to differences in the geometric object of reference.

Indices refer by contiguity in space, time, or deriving from a common substrate. A simple correlation can therefore be the ground for indexical reference. A lipstick smear on a man's shirt collar can be a troublesome indication to his wife, a urine scent on a branch can be a sexual index to a female lemur, and the mobbing call of a small bird can indicate the present of a raptor. What gets correlated and how (accidental, cultural, evolutionary) is arbitrary, but the fact of correlation is not.

A rat in a Skinner box pressing a bar in response to a bell in order to get a water reward has learned that the bell is an index of the state of the apparatus even though this pairing was the whim of an experimenter. The arbitrary pairing doesn't make the one a symbol of the other. Repeated pairing over the course of generations in the evolution of a species can similarly be the basis for an innate tendency to interpret something indexically. This is the case for the indexicality of a vervet monkey alarm call sound and its correlation with the presence of a type of predator and the urge to engage in an appropriate defense activity or escape behavior. Conventionalized indices are also quite common. For example, consider the white line painted down the middle of two lane roads. Though it is a conventionalized sign it refers indexically, *not* symbolically.

However, by virtue of an unfortunate shorthand it has become standard terminology to call most conventional sign vehicles symbols. Thus current vernacular habitually terms alphanumeric characters symbols. This usage reflects the fact that they have been explicitly developed over millennia to express symbolic relations. But when your computer begins randomly spewing alphanumeric characters onto your screen they are indices of a malfunction, not symbols of anything. As Peirce recognized, symbolic reference involves a conventional type of sign vehicle that additionally represents its object of reference in a conventionally-mediated way (Peirce 1931). Something can be considered symbolic, then, only if the property determining its relationship to what it refers to is also a convention. Symbols are in this sense doubly conventional. So arbitrarity, by itself, is not diagnostic of symbolic reference. Nor can it be a critical defining feature of language.

Elsewhere (Deacon 1997, 2003) I have argued that although innate iconicity and indexicality can evolve by natural selection, symbolic reference cannot. This is because of their displacement from features shared with what they represent. Symbols lack the reliably repeated associations between properties that natural selection requires. This explains why there are no innate words, only innate calls (like laughter or sobbing). These are linked to reliable emotional states and characteristic external conditions, which reliably elicit these states.

This requirement has other important implications about language evolution, however, that are not generally recognized. Grammatical rules are even more abstract and less reliably correlated with anything in the brain or in the world than are words. In particular, the surface properties of utterances that provide the grammatical and syntactic information required to interpret a sentence are even less directly correlated with any physical property or relation in the world than are words. So they should be even less likely to arise as a product of biological evolution.

Yet the evolution of the capacity to communicate symbolically has clearly occurred during the course of human prehistory. We humans are the only species that regularly and reliably uses symbolic communication, and even with significant brain damage and mental impairment it is often still possible for people to have some linguistic facility. In contrast, even with extensive training, other quite intelligence species (e. g., apes, dolphins, and possibly parrots) can only acquire very minimal symbolic communicative abilities. This implies that there must have been significant atypical modifications to human brains in the course of their evolution to adapt them to the demands of symbol acquisition and use. So although there can be no innate symbols, there can be evolution to make the acquisition and use of symbolic communication comparatively easy. In turn, however, the regular use of symbolic communication and reasoning over our protracted evolutionary past as a symbolic species has almost certainly changed the ways we humans use even those cognitive abilities that long predate our symbolic awakening. These evolved modifications of human mental capacities have given rise to an unprecedented symbolic niche – culture – that forms the ubiquitous semiotic ecosystem in which we develop in response to. This atypically modified neurology and radically restructured social-ecological context together are responsible for the unprecedented deviation of human biology from the biology of effectively every other species on earth. So the virtual semiotic world of symbols in which we live and to which we have been innately predisposed and developmentally shaped has produced what I describe as our distinctive human symbolic nature.

2. How the Disembodied Became Embodied

To begin to understand the cognitive and neurological adaptations that aid symbolic thought and communication it is useful to first ask: Why is symbolic reference intrinsically difficult for non-human species?

One reason is that learning a symbolic relationship is a bit like cracking a code. One not only needs information about what refers to what, but also needs to understand the system of indexical relations linking symbols to one another and how this system relates to the physical world of properties, objects, and relations. This is because symbolic reference is intrinsically systemic and virtual. Learning correlations between symbols and objects is a start, but one must recognize that this is only a clue to the hidden logic of symbol-symbol (token-token) relationships (i. e., a network of indexical relations such as a linguistic lexicon). Recognizing the systemic correlations between symbol-symbol relations and relationships between properties and events in the real world requires the capacity to transfer relational information from one cognitive context to another quite different and abstract one. This demands a higher-order form of learning, something like an "insight," in which one learns how to re-use selected aspects of what has been learned in new ways.

Insight learning was first systematically studied by a Gestalt theorist: Wolfgang Kohler (1925). He was interested in how apes might problem-solve in a novel context in which the solution requires using previously acquired skills in novel combinations. For this he created "puzzles" in which trial and error problem solving would not have worked, such as piling boxes on top of one another and climbing on them to reach a suspended banana. To succeed it was necessary for the chimpanzee subject to be able to mentally experiment with new combinations of already understood relationships before enacting a plan of action. As a result, after a period of frustrated trial and error, one chimpanzee (Sultan) was seen to suddenly and deliberately arrange things to achieve the result, without trial and error approximations.

The role of insight learning with respect to language acquisition is strikingly exemplified by the account of Helen Keller's discovery of the symbolic nature of language (1905). Blind and deaf from a very early age, she had still not acquired language by early middle childhood. Her tutor, Anne Sullivan, eventually helped her acquire language abilities using a version of finger spelling that was impressed on her hand. Though Helen had acquired a modest set of signs that she could use to identify objects, the point at which she discovers their symbolic function, as opposed to just their indexical correlation with immediately touched objects, is described as a momentary insight. In an event that both Helen and Anne recount in their memoirs, it was an emotionally charged interaction taking place at a water pump that caused Helen to become aware that the signs she already knew constituted and interdependent system of relations that could be used to communicate about things and events not immediately present. In effect, she restructured knowledge that she had previously acquired into a system rather than merely a collection of correlations.

The transition from the one-to-one correlational relationships that is the ground of indexical reference to the system-to-system relationships that ground symbolic reference, as occurred in Helen Keller's epiphany, is not merely learning. It is rather a restructuring of existing knowledge due to the recognition of a previously unnoticed global relational iconism. So the ability to utilize higher-level relational thinking across different cognitive tasks and domains is essential to symbolic communication and reasoning because of the way symbolic reference is mediated by system-to-system correspondences. In other words, it is the recognition that the relational properties among symbol tokens abstractly mirror the abstract form of the relationships among properties, objects, and events in the world.

Recently this has become investigated in terms of a more general capacity, sometimes referred to as transfer learning. It is implicated in a variety of cognitive capacities. These include thinking in terms of analogies, understanding indirect inferential relations, dealing with complicated combinatorial relationships, and using information acquired in one domain to reason about problems in a very different domain. Importantly, all of these cognitive operations place a heavy burden on prefrontal cortex functions (e. g., see Deacon 1997; Vendetti and Bunge 2014; Yarkoni et al. 2011; among many others). Likewise studies attempting to directly test the cognitive-neural demands of making the shift from indexical to symbolic interpretations of the same relationships (e. g., Nieder 2009) have specifically shown the relevance of these prefrontal-dependent capacities for the origins of symbolic capacities.

In my 1997 book *The Symbolic Species* I review evidence from comparative neuroanatomy that suggests that major quantitative changes in the proportions of different human brain structures reflect adaptations for the unusual cognitive demands imposed by symbolic communication. In summary, I showed how embryological divergence of human brain / body proportions as compared to our close primate relatives altered axonal competition during development, favoring connections from relatively enlarged structures. The result was that reduced peripheral connections enabled structures less directly linked to the sensory-motor periphery to outcompete other connections. I predicted that this would have a number of structural-functional consequences. These should include relative enlargement of prefrontal and probably parietal cortex compared to peripherally specialized areas, motor cortex axons invading the nucleus ambiguous (which innervates laryngeal muscles), prefrontal connections displacing cortico-cortical and cortico-striatal projections from other systems, prefrontal-cerebellar connectivity increasing, and other less relevant changes.

In other words, human brains and language co-evolved so that languages were modified by selection favoring learnability and ease of use (via comparatively rapid historical change) and brain functions were modified by selection favoring the special learning and production demands of language (via comparatively slow evolutionary change). One important caveat to keep in mind, however, is this difference in the rate at which things change in culture and biology.

For example, if we compare the amount of time that it takes for a language to split into mutually uninterpretable divergent forms to the amount of time it takes for large mammals like ourselves to split into distinct species unable to interbreed – i. e., thousand versus hundreds of thousands of years respectively – then we can assume at least two orders of magnitude of rate difference. Thus there will be perhaps hundreds of fundamental changes in the structures of human language that only collectively affect selection with respect to common attributes. This means that rather than human brains reflecting specific structural features of language, only the most invariant sensory, motor, attentional, and mnemonic functions will have been selectively favored for their symbolic-linguistic contributions.

With respect to the symbolic cognition problem, then, one of these anatomical differences stands out as specifically relevant: prefrontal cortex expansion. The implication I draw from the coincidence of the distinctive prefrontal expansion in humans and the intense demand placed on transfer learning capacities is that this distinctively human neurological deviation is an adaptation evolved to ease the acquisition and use of symbolic communication and reasoning. But how could this have come about? Did brains become restructured for other reasons and just coincidentally provide the support for this unprecedented learning capacity?

I believe that this apparent “coincidence” has a simpler explanation. These anatomical changes reflect the demands of symbolic communication because they were favored in a context in which it was necessary to acquire and use symbolic communication in order to successfully survive and reproduce. What began as a minimal capacity for symbolic communication (which experiments have shown in apes) supported a very minimalistic form of symbolic social communication, but its value for group success and individual survival and reproduction became a force for both increased reliance on symbols and therefore increased demand on the neurological substrates that this required.

3. Neural Adaptations to a Symbolic Niche

Once symbolic communication became critical to hominid life it effectively became an artificial niche to which hominid cognition had to adapt. I argue that the changes in regional brain proportions and connections, briefly described above, exemplify ways that hominin biology was altered to succeed in this anomalous niche. Analogous to the way that beavers bodies have become morphologically and physiologically adapted to the aquatic niche that beavers create, human brains have become adapted to the special demands of living in the symbolic niche they collectively create. And even the ecological niche that humans inhabit has been modified radically by the technological consequences of our symbolizing. So both human brains and the epigenetic context that shape how these unusual capacities are interdependently shaped into our mature mental predispositions are radically unlike what is found in any other species.

So how are we to characterize the distinctive nature of humanness if it is not possible to untangle the biological from the symbolic? One common response has been to give up the effort and to argue that any simple neo-Darwinian approach is made useless by this irreducible interdependence (e. g., Ingold 2007). But it would be misleading to further conclude that this semiotic-biological causal entanglement has produced a human mode of being that is entirely open-ended and lacks intrinsic constraints. Indeed, despite the unprecedented diversity of human social arrangements and languages, these distinctively human domains are nevertheless also statistically quite constrained. This is reflected in strong central tendencies – rather than some set of universals or list of common attributes – that independently have emerged again and again in human social arrangements, rituals, belief systems, and ways of communicating.

The approach I will take in the remainder of this essay is not, then, to attempt a survey of human social and psychological commonalities. The question I will instead address is: "What distinctive human predispositions can be inferred from our knowledge of this semiotic-biological foundation?" And specifically, I will focus on ways that the more or less virtual constraints imposed by our symbolic heritage have become physiologically embodied in ways that make them inseparable from what is considered biological.

4. Neither Nature nor Nurture

The first of these I will consider are those predispositions that are critical supports for symbolic-linguistic communication. These follow from the underlying semiotic support that is necessary to ground symbolic reference (as discussed above); specifically, the dependency of symbols on indexicality.

Because symbolic relations are indirect and "virtual" – constituted by symbol-symbol relations – an isolated symbol cannot determine reference to anything outside this symbolic domain. This has led to an extended history of arguments over the so-called symbol-grounding problem. I believe that this problem only appears to present a dilemma because symbolic reference is treated as primitive and simple. The dilemma disappears when symbols are understood as higher-order semiotic relations embedded in a context of indexical and iconic modes of reference.

Divorcing linguistic analysis from all forms of semiotic analysis except this simplified conception of symbolic reference, has also made it appear as though the highly systematic structure of language is also arbitrarily imposed. This has led to a half century of irresolvable nature / nurture debates concerning the possible locus of its cause. At one extreme, this structure has been attributed to innate sources of knowledge: nature (often described as universal grammar). Whereas at the other extreme, it is attributed to communicative habits and conventions that spontaneously develop in different societies: nurture. The innatist approach is criticized for being biologically implausible, while the social convention approach is criticized for being unable to account for the remarkable universality of many aspects of language structure. So is the resolution some combination of nature and nurture?

I have argued (Deacon 2003, 2011, 2012) that neither nature nor nurture nor even some combination of these provide an adequate solution to this debate. These options fail to notice an entire third realm of causal influences that results from the oversimplified conception of symbolization. This is the realm of semiotic constraints that arise due to the necessary semiotic infrastructure supporting symbolic reference.

Consider one of the most fundamental universals: the basic combinatorial nature of a sentence, or to be more technically accurate, the requirements for predication (which we might describe as communicating about something specific). Why is communicating linguistically intrinsically combinatorial? All languages produce structures that we recognize as sentences which either explicitly or implicitly combine at least two functionally different components. I believe that this necessarily follows from two important semiotic constraints. First, as noted above, symbol tokens mark positions within a systematic network of relations between symbols. As Saussure recognized, signifiers and signifieds (e. g., words and their meanings) are primarily markers of relative difference in relation to each other, independent of any individual real world binding to specific objects, events, or properties. Reference to individual facts of the world requires indexicality with its factual contiguity.

This dyadic sentential requirement derives from the inability of symbols to refer beyond the domain of other symbols without being additionally provided with indexical linkage. By itself a symbol token, like an isolated word, just pick out a position in the network of symbol-symbol associations. Only proper names have a specific link to a specific entity. So for a symbol to additionally have reference outside this virtual domain of symbolic associations it must be linked to an index or something that functions indexically. Consider someone uttering the word ‘hard.’ By itself it just brings to mind related associations, e. g., to words like soft, solid, difficult, and so on. But uttering the word and at the same time tapping on the table top with one’s knuckles communicates that this particular surface is hard. The tapping is an index because of its immediate physical connection to the table. But this is not all. If the tapping were to take place minutes after the utterance there would be no such reference communicated.

This demonstrates that there is a second indexical feature involved. The physical-temporal correlation between the tapping and the utterance also is interpreted indexically. In this way the combination provides a transitive indexical “bridge” linking the abstract symbol to the specific hardness of the real physical table. But notice that the tapping could have been replaced by the phrase “This [table] is . . .” – perhaps also with the addition of a pointing gesture.

This constraint reflects fundamental features of both symbols and indices. Indexicality requires both the co-presence with a symbol token and embeddedness in a specific physical context. Contiguity of an index to a symbol (e. g., adjacency) provides both language-internal indexicality and language-external grounding. This dyadic linkage between semiotic functions in sentences and phrases within sentences, reflects the constraints on indexicality. This is what dictates phrase structure and its many syntactic correlates, such as the necessity of “merging” functionally different words into a higher-order unit, limitations on between-phrase function-word movement, and dependency relations, to mention a few. Because of the factual contiguity constraint of indexicality words functioning symbolically and indexically must be immediately linked, for the same reason that words and manual indices (such as the tapping described above) must be factually linked (though also employing iconic relations, such as gender agreement can provide some flexibility on what counts as adjacency). This imposes significant limitations on what can be “merged” with what in a phrase or clause, what parts of speech can be moved with respect to others, and what constitutes an embeddable phrasal unit.

This has an important bearing on questions concerning knowledge of language structure. Specifically, it suggests that grammatical roles and their associated syntactic constraints can be "discovered" both historically as new languages emerge and developmentally because there will be clear feedback concerning adequate or ambiguous specification of reference (Deacon 2011, 2012). The oftcited "poverty of the stimulus" argument, which suggests that there is nearly a complete lack of corrective feedback concerning grammatical and syntactic errors in early childhood, is simply looking in the wrong place for the appropriate source of feedback.

5. Pointing and Joint Attention

Young children have a bit of an innate head start when it comes to their ability to learn the constraints of indexicality. In the half year prior to acquiring their first words (another uniquely human predisposition discussed below) their communication with caregivers is aided by a predisposition to use their outstretched arm to point, often coupled with a non-linguistic vocalization such as whining to indicate an unfilled desire with respect to some object or activity. In addition, they quickly learn that a change in the direction of gaze of a caretaker is predictive of their future behavior with respect to something in that direction.

These distinctively human adaptations aiding cooperative indexicality are well known, and have become a major focus of comparative study. Whereas even human infants easily and spontaneously develop gaze following, pointing behaviors, and shared referential predispositions at an early age, well in advance of language acquisition, few other species come close to this level of performance, even with explicit training. This early indexical sophistication is an important precursor for the development of language. A sophisticated prior understanding of the constraints critical to unambiguous shared indexical reference provide a critical scaffold for the development of the core attributes of this universal grammatical constraint.

The constraints on successful indexicality are thus learned prior to speech and effectively transferred to use with words. Though the development of sophistication with indexicality will continue to be learned in the context of early language acquisition this mostly requires discovering how each particular language encodes these functions in words. As the first words are acquired (initially as vocal indices correlated with gestures) the functional forms of grammar and the structural constraints of syntax are in many respects already known. Applying this knowledge to language use requires the sophisticated transfer learning abilities that have also evolved, but not innate knowledge of grammar.

6. Vocal Skill and Mimicry

Another distinctive characteristic of humans that sets our species apart from essentially all other land mammals is our capacity to produce complex vocalizations that involve the articulation of the mouth and tongue with precisely synchronized control of the lungs and larynx. The innately produced calls of other land mammals are comparable to human laughter and sobbing, in being stereotypically structured and invariantly linked with specific arousal states. This mammalian limitation is a consequence of the fact that the descending neural control for the tongue, jaw, and facial muscles is distinct from that controlling the larynx and lungs. This is because the muscles of the mouth and face need to be under complex voluntary control in order to be able to adapt moment to moment to the variety of foods that need to be processed. In contrast, pharyngeal, laryngeal, and lung muscles need to function the same way time after time with each swallowing or breath, and need to do so infallibly and automatically. As a result, in the vast majority of land mammals these automatic systems are controlled locally in the brainstem, with little or no cortical input, as part of the visceral-motor system.

Species besides humans that have some skilled control of vocalization are only found among birds and cetaceans (the group including dolphins and whales). In these groups the production of sound uses structures other than a larynx. These include muscles constricting the pathway through the sinuses leading to the blow hole in cetaceans, and the muscular syrinx at the branch point of the bronchi in birds (see Deacon 1997 for details).

Along with these motor control adaptations, humans are predisposed to imitate the vocalizations of other humans. This is of course an important predisposition for early language acquisition, since each human language requires the ability to understand and produce many thousands of language-specific sound combinations (e. g., words). Although other species exhibit some mimicry capabilities, the human capacity is an order of magnitude more complex. Interestingly, almost all other species with significant imitative abilities exemplify this capacity in the aural-vocal domain, and have very limited behavioral mimicry capabilities. This phylogenetic bias probably reflects the fact that behavioral mimicry requires a complex visual-behavioral transformation to compensate for the mirror-image effect that reverses left and right, whereas sound mimicry requires no such transformation.

7. Narrative Memory

In all species of mammals learning depends on one or the other of two distinctively different mechanisms for establishing long-term stable memories, each depending on quite distinct neural substrates (e. g., see Baars and Gage 2007). The acquisition of skills is accomplished by repetition of an activity, which progressively improves precision and efficiency of the activity and increasing its automaticity and reducing the need for consciously monitoring production. It is generally assumed that repetition progressively strengthens some complex synaptic pathways and weakens others. Thus retention and recall of this information is facilitated by the way that the signaling has become canalized by redundant synaptic strengthening. Since skill learning is particularly important for motor systems (even though also necessarily coupled with sensory feedback), the major brain systems involved mostly involve a frontal cortex to basal ganglia to thalamus to cortex loop, and a similar cortex to cerebellum to thalamus to cortex loop. Damage to structures or connections comprising these loops, significantly impairs this sort of memory formation. This mnemonic strategy is often called procedural memory for these reasons. It exemplifies the general principle that mnemonic strength and accessibility is a function of statistical redundancy.

In contrast, it is also critical to be able to store and retrieve experiential information in contexts where repetition is not possible. What has been called episodic or declarative memory is memory for events or episodes that occurred once, uniquely, are not repeated, and involve little in the way of repeatable actions. This requires the generation of redundancy of a different sort: redundancy of associations. This creates memory traces for singular experiences by correlations between features. Thus when we try to recall a specific experience from our past, it is generally necessary to triangulate to it using correlated associations, involving dates, places, typical social frames, and so forth. This form of mnemonic redundancy is formally orthogonal to the logic of procedural memory, and is thereby supported by quite distinct neural substrates. Thus, episodic memory is generated by neural circuits linking sensory cortices with the hippocampus and hippocampal damage significantly impairs the ability to consolidate new episodic memories.

Because of this functional segregation of these mnemonic systems language can play an interesting mediating role. Indeed, it has become the foundation of an unprecedented new form of memory. Early in the process of language acquisition articulatory and syntactical combinatorial skills are acquired procedurally. In contrast, the symbolic reference that constitutes word meanings and their penumbra of semantic and experiential values are necessarily acquired. Because of this dualistic use of mnemonic systems language enables each mnemonic system to reciprocally cue the other. Narrative memory is the result. It forms the basis for promising, reasoning, theorizing, creating our identities, histories, politics, and art. Essentially, every form of socially maintained pragmatic knowledge, from religious belief to technology, is built from a growing matrix of narrative forms.

So although the neural substrates supporting these distinct mnemonic systems have not been fundamentally altered in human evolution from the ancestral primate condition, human cognition has been radically restructured by this novel mnemonic capability. The effects of this on the nature of human identity, agency, and social organization, as well as on the capacity of social groups to acquire and preserve complex knowledge over time, cannot be over-estimated.

8. Emergent Emotions

The consequences of these unprecedented adaptations for symbolic cognition weren't merely cognitive and linguistic, however. These capabilities have also incidentally produced uniquely human forms of emotional experience. Like the unique functional synergies that have re-organized the way that ancient mnemonic systems can be used, symbolic capacities have similarly re-organized the functions of the emotional systems of the brain. This has given rise to a whole class of human-unique emotional capacities (Deacon 2006). These might more accurately be described as symbolically modulated emotional relationships that also are realized by neuronal systems that we humans share with most other mammals.

Because symbol tokens represent their content indirectly and without sharing attributes or direct correlations with the thoughts they convey, the salience and intensity of their emotional correlates are also substantially reduced. This enables symbols to be combined and juxtaposed in many more diverse ways than other sorts of signs. This combinatorial freedom can lead to the expression of emotional interactions that could not otherwise occur. Because the correlated emotions aroused by symbol combinations are of low intensity they too are more easily manipulated and combined in novel ways. So it's not that we have evolved novel neurological systems for emotional expression, but that these processes can be set into novel synergistic and antagonistic and complementary combinations that would be very unlikely to occur in the absence of symbolic processes.

So what are some plausible candidates? Awe, nostalgia, righteous indignation, aesthetic appreciation, humor, irony, eureka . . . All these involve unusual juxtapositions of more basic emotional dynamics, likely activated differently in the distributed structures responsible for emotion, including differences in homologous structures in the two hemispheres. So not only can this involve the separate circuits that handle different arousal and hedonic states, but the bilaterality of these systems may also allow novel combinatorial interactions of otherwise mutually incompatible emotional dynamics in response to the flexibility of symbolic manipulation. This may help to explain the human fascination with activities that symbolically tweak our emotions in unusual and surprising ways.

For two prominent examples consider humor and artistic aesthetics. Humor involves a distinctive emotional replacement logic: a rapid shift of arousal from one state of expectation (often with tension) to another that completely dispels the tension. Curiously, this can be driven by purely linguistic twists of logical expectation, as in puns and jokes. This may involve a left to right hemispheric shift of activation because of the typical replacement of a typical logical expectation with a contextually parallel but absurdly unrelated consequence. In contrast, the aesthetic elation that can be elicited by artistic works often involves sustained emotional juxtapositions, rather than alternation. And other more complex emotional dynamics may be involved in the eureka experience of discovering new and surprising connections, the sense of irony elicited by juxtaposed opposites, or the sense of righteous indignation elicited by recognizing the failure to conform to expected norms.

9. Religiosity

Because of this suite of adaptations and the fact that linguistic communication and symbol-mediated cognition are integrated into every aspect of our lives we humans have essentially become symbolic savants (Deacon 1997; Deacon and Cashman 2009). We find ourselves intuitively and irresistibly "looking beyond the surface" for hidden meanings. The cognitive biases that evolved to make symbolic communication seem natural and effortless and quickly becomes the mental tool used to negotiate the vast majority of challenges we face, has likely also radically altered the way we tend to interpret even everyday non-symbolic experience. A linguistic description is an impoverished transcription of the thought that gave rise to it. The perceived sounds are clues pointing to an unseen thought not present to the senses and so must be reconstructed. The sounds and objects present to the senses are not meaningful in themselves, they are what we have to work with as intermediaries to discover the meaning making process that produced them.

The world's many spiritual traditions almost universally depict the existence of a world beyond the immediate physical world that is in some way more fundamental and ultimately determines the events and forms found in the world available to our senses (Deacon and Cashman 2009). Though what constitutes the constellation of beliefs and practices that define "religion" is a matter of contentious debate, in nearly every society we find traditions that assume that there exists a nonphysical world hidden from direct sensory experience. Deacon and Cashman (2009) describe this as the "bilayered world" assumption. Just as we intuitively assume that the words and actions of others are merely the superficial physical manifestations of an otherwise inaccessible agency that is the source of meaning and purpose expressed in these physical manifestations, so too have we come to look upon the happenings in the physical world to be the superficial expressions of some hidden teleology. It is as though we are unable to inhibit this compulsion to see everything in the image of symbols. Is it simply that since infancy we have needed to seek the meaning behind the curtain of the language and culture we are immersed in? Or did our long adaptation to a symbolic niche predispose us to reflexively think of the world we perceive as though it is text that needs to be interpreted, if only one knew how? Either way it has molded us into symbolic savants who incessantly and irresistibly see the world in bilayered terms.

In many respects, then, I consider the human discovery of the use of symbols to be the "original sin." Symbolic abilities have given us access to the knowledge contained in the forbidden fruit, and in this way we have been driven from the obliviousness of a pre-symbolic Eden. It provided access to unique emotions, indirect access to the thoughts and experiences of other minds, and a yearning for meaning in the narrative that is human identity. This transition has left us forever seeking a meaning hidden within a disembodied realm and thinking of the mundane physical world around us as deriving any of its value from this projected meaning source.

10. Relaxation of Selection and Plasticity

How could these many diverse cognitive and behavioral traits have become so functionally intertwined and interdependent as to provide such a novel means of thinking, feeling, and communicating? And how could the diverse brain systems supporting them have come to work in such a tight and unprecedented synergy? This is particularly challenging to explain because this symbolic capacity is in effect an emergent function, not some prior function just requiring fine-tuning.

Our various inherited vocalizations, such as laughter, shrieks of fright, and cries of anguish, are comparatively localized in their neurological control (mostly subcortical) as are other modes of communication in animals. In comparison, language depends on a widely dispersed constellation of cortical systems, each of which can be found in other primate brains, but evolved for very different functions. These brain systems have become collectively recruited for language only because their previously evolved functions overlapped significantly with some processing demand necessitated by language, though evolved for quite different functions altogether.

A related mystery concerns the extent to which this dominant form of human communication depends extensively on information acquired by social transmission. Even for theories postulating an innate universal grammar, the vast quantity and high fidelity of the information constituting even a modest vocabulary stands out as exceedingly anomalous from a biological point of view. How did such a large fraction of our communicative capacity wind up offloaded onto social transmission? And what explains the remarkable reliability of this process? These unprecedented emergent features of brain function and cognition suggest that a co-evolutionary logic alone is insufficient to explain them. Recent investigation of a parallel shift in both complexity and neural substrate in birdsong may, however, be able to shed some light on this.

In a comparative study of a long-domesticated bird, the Bengalese Finch, and its wild cousin, the White-Rump Munia, it was discovered that the domesticated lineage was a far more facile song-learner with a much more complex and flexible song than its wild cousin (e. g., see Okanoya 2004). This occurred despite the fact that the Bengalese Finch was bred in captivity for coloration, not singing. The domestic / wild difference of song complexity and song learning in these close finch breeds parallels what is found in comparisons between other bird species that are song-learners and non-learners. This difference also correlates with a much more extensive neural control of song in birds that learn a complex and variable song through social transmission.

The fact that this behavioral and neural complexity can arise spontaneously without specific breeding for singing is a surprising finding since it is generally assumed that song complexity evolves under the influence of intense sexual selection. In the case of the Bengalese Finch, his source of selection was eliminated by the intervention of human breeders.

In Deacon (2010), I argued that, paradoxically, it was the relaxation of natural and sexual selection on song structure that was responsible for its elaboration in this example. In brief, with song becoming irrelevant to species identification and mate choice in the domesticated lineage, territorial defense, mate attraction, predator avoidance, and so on, the innate mechanisms constraining song were allowed to degenerate. Mutations that resulted in degeneration of these systems and existing recessive alleles producing a less stereotypic song would not have been weeded out. The result would be the reduction of innate biases controlling song production. The domestic song could thus be described as both less constrained and more variable because it is subject to more kinds of perturbations.

But with the specification of song structure no longer strictly controlled by the primary forebrain motor center of the songbird brain (called nucleus RA), other linked brain systems could begin to play a biasing role. With innate motor biases weakened, auditory experience, social context, learning biases, and attentional factors could all begin to influence singing. So the domestic song would be expected to become more variable, more complicated, and more influenced by social experience. These changes are what we observe in the case of the Bengalese Finch.

This is relevant to the human case, because a number of features of the human language adaptation also appear to involve a relaxation of innate constraints, allowing multiple brain systems and extrinsic influences to affect linguistic communication.

The presence of infant babbling, increased variability and skilled modification of vocal behavior, decoupling of vocalization from arousal state, an extensive capacity for vocal imitation, etc., may all be consequences of a parallel relaxation of selection with respect to vocal communication. Freedom from constraint is also an important precondition for being able to correlate learned vocal behaviors with the wide diversity of objects, events, properties, and relationships that language is capable of referring to. It is also a plausible answer to the combinatorial synergy problem of brain functions (discussed above) because it provides an evolutionary route to multi-system coordination.

How might this analogue to the effects of domestication have arisen in human prehistory? Perhaps the most striking clues to an answer come from major changes in body structures and demographics occurring at various points in our hominin ancestry. The first and most obvious is a shift to bipedal locomotion somewhere in the period around 4 million years ago that relaxed selection on the upper limbs and hands enabling more flexible manipulation of objects. This was a precursor to the discovery of how to produce and use sharpened stones to gain access to the rich animal flesh resource that may date to over 3 million years into the past. But what may be the most radical change probably didn't occur until about 2 million years ago. This transition is characterized by a number of correlated anatomical and behavioral changes that indicate a major shift in all aspects of hominin life. Stone tool use becomes ubiquitous, bipedal locomotion becomes fine-tuned to modern forms, body size increases, brain size increases above typical ape levels, jaws and teeth are significantly reduced, and sexual dimorphism is decreased to modern levels. And perhaps most significantly, it is at this point that tool using hominins are, for the first time, found outside of Africa, in Central and Southeast Asia. There were likely other similar migration events occurring subsequently, but the last and most extensive migration out of Africa occurred as recently as 60,000 years ago, as anatomically modern-looking people swept over all of Eurasia to replace previous populations. Each of these events suggests that new levels of flexibility have become available giving rise to yet further phases of relaxation.

There is also increasing genetic evidence of relaxation of selection distinguishing humans from other primates. Although traditional assumptions about the role of genetic change in evolution have tended to focus on mutations that augment some function, evidence is growing that gene duplication and gene loss – including especially loss of non-coding regulatory sequences – has contributed to significant evolutionary change (e. g., Olsen 1999; Hunt et al. 2011).

Human-specific loss of over 500 otherwise highly conserved non-coding regulatory sequences has recently been reported (McLean et al. 2011). This extensive loss of genetic regulation may be a signal of human-specific relaxation of selection and an increased sensitivity to epigenetic and environmental influences.

This argument inverts the claim that increased genetic specification of grammatical knowledge underlies our language capacity and is instead consistent with the explanation of language universals arising from extra-biological sources (such as suggested above). But perhaps the most important implications involve the incredible flexibility of human cognition and behaviors. We largely take this for granted, but in many respects it is one of the most robust and significant aspects of our distinctive nature. As a result, not only are human languages incredibly diverse, but all aspects of human culture show unprecedented diversity compared to anything found in the rest of the animal kingdom. Many of the distinctive symbolic adaptations discussed above reflect this increased openness to developmental and cultural influences that have led many to question the very concept of human nature.

Conclusion

In this essay I have reviewed extensive evidence that the unusual demands of symbolic communication and thought have restructured our brains, have provided an unprecedented degree of behavioral flexibility, and have embedded us in a symbolic ecosystem – culture – that is radically unlike the *Umwelt* of any other species. Symbolization has thereby modified nearly every aspect of what makes us human. The result is that our distinctive "nature" is as much symbolic as it is biological.

Bibliography

Baars, B. J. and N. M. Gage. 2007. *Cognition, Brain, and Consciousness: Introduction to Cognitive Neuroscience*. London: Elsevier Ltd.

Bock, K. E. 1980. *Human Nature and History: A Response to Sociobiology*. New York: Columbia University Press.

Deacon, T. 1997. *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: W. W. Norton & Co.

– . 2003. Universal Grammar and Semiotic Constraints. In *Language Evolution*, ed. M. Christiansen, and S. Kirby, 111 – 139. Oxford: Oxford University Press.

– . 2006. The Aesthetic Faculty. In *The Artful Mind*, ed. M. Turner, and S. Zeki, 21 – 53. Oxford: Oxford University Press.

– . 2009. Relaxed Selection and the Role of Epigenesis in the Evolution of Language. In *Oxford Handbook of Development Behavioral Neuroscience*, ed. M. S. Blumberg, J. H. Freeman, and S. R. Robinson, 730 – 752. New York: Oxford University Press.

– . 2010. A Role for Relaxed Selection in the Evolution of the Language Capacity. *PNAS* 107: 9000 – 9006.

– . 2011. The Symbol Concept. In *The Oxford Handbook of Language Evolution*, ed. M. Tallerman, and K. Gibson, 393 – 405. Oxford: Oxford University Press.

– . 2012. Beyond The Symbolic Species. In *The Symbolic Species Evolved*, ed. T. Schilhab, F. Stjernfeldt, and T. Deacon, 9 – 38. Dordrecht: Springer.

Deacon, T. and T. Cashman. 2009. The Role of Symbolic Capacity in the Origins of Religion. *Journal of Religion, Nature & Culture* 3: 490 – 517.

– . 2012. Teleology versus Mechanism in Biology: Beyond Self-Organization. In *Beyond Mechanism: Putting Life Back Into Biology*, ed. B. Henning and A. Scarfe, 287 – 308. Lanham, MD: Lexington Books / Rowman & Littlefield.

Hull, D. 1986. Human Nature. *Proceedings of the Biennial Meeting of the Philosophy of Science Association* 2: 3 – 13.

Hunt, B. G., L. Ometto, Y. Wurm, D. Shoemaker, S. V. Yi, L. Keller, and M. Goodisman. 2011. Relaxed Selection Is a Precursor to the Evolution of Phenotypic Plasticity. *PNAS* 108: 15936 – 15941.

Ingold, T. 2006. Against Human Nature. In *Evolutionary Epistemology, Language and Culture: A Non-Adaptationist, Systems Theoretical Approach*, ed. N. Gontier, J.-P. van Bendegem, and D. Aerts, 259 – 281. Dordrecht: Springer.

– The Trouble with ‘Evolutionary Biology.’ *Anthropology Today* 23 (2): 13 – 17.

Keller, H. 1905. *The Story of My Life*. In Parts I & II; Part III from the Letters and Reports of Anne Mansfield Sullivan (ca. 1867 – 1936), ed. J. A. Macy. New York: Doubleday, Page & Company.

Kohler, W. 1925. *The Mentality of Apes*. Trans. Ella Winter from the second revised edition. London: Kegan Paul, Trench, Trubner.

McLean, C. Y., P. L. Reno, A. A. Pollen, A. I. Bassan, T. D. Capellini, C. Guenther, V. B. Indjeian et al. 2011. Human-specific Loss of Regulatory DNA and the Evolution of Human-specific Traits. *Nature* 471: 216 – 219.

Nieder, A. 2009. Prefrontal Cortex and the Evolution of Symbolic Reference. Current *Opinion in Neurobiology* 19: 99 – 108.

Okanoya, K. 2004. The Bengalese Finch: A Window on the Behavioral Neurobiology of Birdsong Syntax. *Annals of the New York Academy of Sciences* 1016: 724 – 735.

Olsen, M. 1999. When Less is More: Gene Loss as an Engine of Evolutionary Change. *American Journal of Human Genetics* 64: 18 – 23

Peirce, C. S. 1931. *Collected Papers of Charles Sander Pierce. Vol. II Elements of Logic*, ed. C. Hartshorn and P. Weiss. Cambridge, MA: Harvard University Press.

Vendetti, M. S. and S. A. Bunge. 2014. Evolutionary and Developmental Changes in the Lateral Frontoparietal Network: A Little Goes a Long Way for Higher-Level Cognition. *Neuron* 84: 906 – 917.

Yarkoni, T., R. A. Poldrack, T. E. Nichols, D. C. Van Essen, and T. D. Wager. 2011. Largescale Automated Synthesis of Human Functional Neuroimaging Data. *Nature Methods* 8: 665 – 670.