

A role for relaxed selection in the evolution of the language capacity

Terrence W. Deacon¹

Department of Anthropology, University of California, Berkeley, CA 94720

Explaining the extravagant complexity of the human language and our competence to acquire it has long posed challenges for natural selection theory. To answer his critics, Darwin turned to sexual selection to account for the extreme development of language. Many contemporary evolutionary theorists have invoked incredibly lucky mutation or some variant of the assimilation of acquired behaviors to innate predispositions in an effort to explain it. Recent evodevo approaches have identified developmental processes that help to explain how complex functional synergies can evolve by Darwinian means. Interestingly, many of these developmental mechanisms bear a resemblance to aspects of Darwin's mechanism of natural selection, often differing only in one respect (e.g., form of duplication, kind of variation, competition/cooperation). A common feature is an interplay between processes of stabilizing selection and processes of relaxed selection at different levels of organism function. These may play important roles in the many levels of evolutionary process contributing to language. Surprisingly, the relaxation of selection at the organism level may have been a source of many complex synergistic features of the human language capacity, and may help explain why so much language information is "inherited" socially.

brain | Darwin | evodevo | complexity | domestication

Language is both a social and biological phenomenon. The capacity to acquire and use it is a unique and distinctive trait that evolved in only one species on earth. Its complexity and organization are like nothing else in biology, and yet it is also unlike any intentionally designed social convention. Short of appealing to divine intervention or miraculous accident, we must look to some variant of natural selection to explain it. By paying attention to the way Darwin's concept of natural selection can be generalized to other systems, and how variants on this process operate at different interdependent levels of organism function, explaining the complexity of language and the language adaptation can be made more tractable.

Darwin's theory of natural selection is based on three widely acceptable characteristics of organism reproduction. In the early winter of 1838, after reading Thomas Malthus' "Essay on Population," Charles Darwin wrote the following lines in his E Notebook: "Three principles will account for all: (1) Grandchildren like grandfathers; (2) Tendency to small change...especially with physical change; (3) Great fertility in proportion to support of parents" (ref. 1, p. 58).

In the most general terms, these correspond to duplication-multiplication, spontaneous variation from the original, and the surfeit of reproduction that will inevitably reduce this variety via competition for scarce resources. Darwin's final refinement was to recognize that, given inevitable culling, the conditions of survival (and particularly, reproduction) would differentially reduce this variety in a way that favored variant traits best suited for that context—adaptation. Darwin recognized that *irrespective of the mechanisms involved*, if these conditions are present, a lineage will tend to become adapted to local conditions if given sufficient time and generations. This was a remarkably simple recipe for biological change, and yet its implications were enormous and counterintuitive. As one critic of *On the Origin of Species* (2) was to write: "In the theory with which we have to deal, Absolute Ignorance is the artificer; so that we may enunciate as the fundamental principle of the whole system, that, in order to make a perfect and beautiful machine, it is not requisite to know how to make it" (ref. 3, p. 217).

Adaptation is the natural counterpart to functional design, but the idea that exquisite biological design might be achieved in the absence of any information about the context of use seemed absurd. Deeply ingrained intuitions, gained through the difficult experience of designing and constructing even simple artifacts and machines, made it unquestionable that only considerable planning and knowledge about the relevant properties of the materials and tasks involved could yield reliable functional outcomes. Moreover, the difficulties encountered multiply geometrically with increasing complexity because of the way that changing one component can interfere with the relationships to others. Given the fact that organisms are constituted by vastly many complicated systems of chemical and cellular interactions, this difficulty has led critics to conclude that precisely because it is a blind and mindless mechanism it should be less capable of giving rise to adaptive functionality the more complex the system. Thus, such highly complex functional capacities as human cognition and language would intuitively seem to be the least evolvable of life's products. Indeed, so-called "intelligent design" critiques of Darwinism have focused on far simpler molecular and cellular mechanisms to make their argument that the complexity of organism design is not evolvable, indirectly implying that our vastly more complex cognitive abilities are all the more beyond the explanatory power of natural selection theory.

For these reasons, since Darwin's time, the human language capacity has been a perennially cited paragon of extreme complexity that defies the explanatory powers of natural selection. And it is not just critics of Darwinism who have argued that this most distinctive human capacity is problematic. Alfred Russell Wallace—the co-discoverer of natural selection theory—famously argued that the human intellectual capacity that makes language possible is developed to a level of complexity that far exceeds what is achievable through natural selection alone. While fiercely defending natural selection theory with respect to the traits of other species, he argued that in the case of humans, "natural selection could only have endowed the savage with a brain a little superior to that of an ape" (ref. 4, p. 392). And Charles Lyell—who personally promoted Darwin's work and generally supported the evolutionary perspective—also worried that language was just too complex to have evolved by natural means (5, 6). The vast vocabulary and baroquely structured grammar and syntax of even the most simple of natural languages is orders of magnitude more complex than any other species' communication system, and the capacity this provides for expressing highly esoteric concepts and conveying aesthetic experiences seems far removed from anything with direct adaptive consequence.

Despite the unimpeachable success of Darwinian theory in the 150 years that have elapsed since the publication of *On the Origin of Species* (2), language still poses challenges for evolutionary biology. The challenge is probably best exemplified by how language origin

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, "In the Light of Evolution IV: The Human Condition," held December 10–12, 2009, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and audio files of most presentations are available on the NAS Web site at www.nasonline.org/SACKLER_Human_Condition.

Author contributions: T.W.D. wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

¹E-mail: deacon@berkeley.edu.

is still being explained by many highly respected theorists. Take for example Noam Chomsky, who is arguably the most influential linguist of the 20th century. He has reasoned that human language competence could not have been the product of natural selection, even though he believes that it evolved as an inherited biological trait. Its special features, such as its recursive organization, and the often-baroque ways this property is reflected in the various acceptable and unacceptable syntactic operations of a given language, do not according to him facilitate any communicative function (7). Indeed they seem on the surface to be reflections of a tendency for systematization of language-unique principles of structural coherence and systemic consistency that may have more to do with the generativity of thought than with communication (8). Few if any of these features can be justified in terms of any direct contribution to reproductive benefit.

Of course, nonadaptive traits, functional compromises, and inefficiency are also common to other biological adaptations. So this does not in itself disqualify the human language faculty as a biological adaptation honed by natural selection. But an innate capacity that appears to be highly complex in ways that mostly tend to impede functional utility requires special explanation.

Chomsky's nonadaptationist view is not, however, widely accepted, even by those who otherwise promote his strong nativist approach to linguistic theory. For example, Steven Pinker (9) has eloquently argued that the structural complexity of language implicitly demands a natural selection explanation. He echoes the general assumption that *only* the process of natural selection can generate such well-fitted functional complexity in biology. No mere side effect or accidental genetic damage can be expected to exhibit anywhere near the complexity and utility of language or the human predisposition to acquire it. The very complexity of this capacity is thus taken as evidence of the operation of extensive natural selection.

Darwin himself fretted over the possibility that natural selection alone might be incapable of accounting for exaggerated functional complexity in nature. In a letter he wrote to Asa Gray shortly after the publication of *On the Origin of Species* (2), he admits that "the sight of a feather in a peacock's tail, whenever I gaze at it, makes me feel sick!" (10). Despite the spectacular and elaborately formed details of this adornment, it was a burden that negatively impacted health and survival and so could not have been subject to natural selection with respect to the environment. But it was the extravagance of traits such as this, despite their lack of utility, which suggested to Darwin an approach to the challenge of explaining human mental capacities.

In the case of the peacock tail, and other similar traits, Darwin realized that, indeed, something other than natural selection with respect to environmental conditions was responsible. Recognizing that reproduction rather than individual survival was the critical factor in evolution, he argued that competition with respect to reproductive access (sexual selection) could result in runaway selection on certain traits, independent of their environmental suitability. Darwin argued that a display feature or fighting ability that led an individual to outcompete others in gaining access to mates would also favor proliferation and evolutionary exaggeration of these traits, even at some cost to individual health and survival. Analogously, he postulated that selection with respect to sex might also explain such extravagant and highly divergent traits as human language. In his book *The Descent of Man and Selection in Relation to Sex* (11)—which is typically referred to by only the first half of its title—Darwin argues that language and other human traits that appear exaggerated beyond survival value can be explained as consequences of sexual selection. So, for example, he imagines that language might have evolved from something akin to bird song, used as a means to attract mates, and that the ability to produce highly elaborate vocal behaviors was progressively exaggerated by a kind of arms-race competition for the most complex vocal display.

Unfortunately, Darwin's speculations in this respect were most effectively criticized by the worst of all possible opponents: the co-discoverer of natural selection, Alfred Russell Wallace. Wallace was scandalized by Darwin's sexual selection theory, considering it Darwin's greatest error, because it appeared to admit a subjective factor into evolutionary theory. Indeed, it appeared to elevate aesthetic appreciation to the status of a significant factor in evolution. Wallace's alternative theory to account for exaggerated display traits relied instead on explanations that invoked incidental physiological mechanisms in males and the need to suppress their effects in females, to avoid predation. But when combined with his strong anti-Lamarckian views, Wallace's denial of Darwin's sexual selection account of these extreme human traits appeared to leave him with no other conceivable mechanism capable of explaining them. He instead abandoned a physical account altogether and infamously invoked a spiritual influence, suggesting that "some intelligent power has guided or determined the development of man" (ref. 12, p. 350).

Wallace was of course wrong in his denial of the plausibility of sexual selection, although not completely wrong to doubt that aesthetic appreciation or combative prowess were the primary factors. It took a century to recognize that the theory needed to be based instead on asymmetries of parental investment in offspring care between the sexes (13). Today, sexual selection theory is again considered an important adjunct to the theory of natural selection; however, its reinstatement has not resuscitated the power of Darwin's account of language origins.* Even though Wallace's critique of sexual selection has been answered and its power to explain the evolution of certain exaggerated traits is now recognized, there are strong reasons for doubting its relevance to this most distinctive of human traits. This is because sexual selection inevitably produces complementary divergence of male and female traits, as is exemplified by peacock tails and moose antlers, which are exhibited only by males. Though there are indeed a few highly divergent traits distinguishing women from men (e.g., patterns of fat deposition in breasts and hips, etc.), the sexes differ only very subtly in their intellectual and language abilities. Therefore, accounting for the extravagant complexity of language in terms of sexual selection requires explaining why it lacks this otherwise-ubiquitous mark of extreme sexual dimorphism.

For the most part, however, worries about the sufficiency of natural selection theory to account for our language capacity have simply been ignored by contemporary theorists. Some of the more prominent approaches to the origins of language avoid the issue of selection altogether by attributing this ability to an astonishingly lucky accident of genetic mutation. Previously, it was noted that Chomsky has attributed this unique capacity to a salutatory event in which this ability arose suddenly and irrespective of honing by natural selection. But archeologists such as Mellars (17) and Klein (18), noting the explosion of cultural variations of stone tool technologies and the first appearance of decorative and representational forms (such as beads, carvings, and cave paintings) between 60,000 and 30,000 years ago, have argued that a sudden major change in brain function (a mutational accident that Klein has characterized as "the brain's Big Bang") could explain this apparent appearance of recognizably modern human activities.

This willingness to appeal to lucky accident as the primary explanation for this distinctive trait is in many respects a symptom of the problem, not an explanation. Worse, it is an approach that could easily backfire. The appeal to pure accident, e.g., a "hopeful monster" mutation, to explain the evolution of such a highly complex and distinctive trait is the biological equivalent of invoking a miracle. Although neo-Darwinism is indeed based on the assumption that accidental genetic changes contribute to the phylogenetic diversification of traits, this does not imply that complex functional

*There are, nevertheless, contemporary theorists who have offered variants on Darwin's proposed sexual selection account of language origins (see, e.g., refs. 14, 15, and 16).

organization arises by accident. This overemphasis on the creative role of variation reflects a tendency to downplay the fact that what varies must be generated by processes of reproduction and development. It is the spontaneous variation of these generative processes that provides the raw material from which natural selection sculpts, so to speak, and so the properties of these generative mechanisms must also be considered. This expansion of focus has given rise to a view of the evolutionary process often called *evodevo*, because it specifically takes account of the constraining and biasing influences of these generative processes. Highlighting this aspect of the evolutionary process will be the focus of this essay.

To explain the origin of the highly structured human-unique adaptation inevitably requires addressing Wallace's challenge concerning the complexity and apparent nonadaptive aspects of these features. It is significant, then, that theorists who view language functions as products of natural selection have turned to a somewhat indirect variant of the theory to account for the many details of language structure. Most commonly, this is involves an appeal to what has come to be called the "Baldwin effect" after one of its late 19th-century architects, James Mark Baldwin (19).[†] This was a variant of natural selection theory that theoretically might lead to pseudo-Lamarckian effects, such that the functional utility of a specific acquired habit of behavior (e.g., a language behavior) could eventually come to be replaced by a fortuitously arising (e.g., via chance mutation) innate analog. The appeal to this theoretical variant of natural selection—which is still a subject of debate concerning both its distinctiveness and presumed efficacy (e.g., 23–26)—exemplifies the special problems that the extravagant complexity of language poses for natural selection.

A variant of this argument is proposed in Deacon (27), where it is suggested that the regular use of prelinguistic symbolic communication (or protolanguage) created what amounts to a socially constructed artificial niche that in turn imposed novel cognitive demands on hominid brains. This early articulation of what has come to be called "niche construction" theory (28) argues that, analogous to the evolution of beaver aquatic adaptations in response to a beaver-generated aquatic niche, a constellation of learning biases and changes of vocal control evolved in response to the atypical demands of this distinctive mode of communication. To the extent that this mode of communication became important for successful integration into human social groups and a critical prerequisite for successful reproduction, it would bring about selection favoring any traits that favored better acquisition and social transmission of this form of communication. Unlike Baldwinian arguments for the genetic assimilation of grammatical and syntactic features of language, however, the niche construction approach does not assume that acquired language regularities themselves ever become innate. Rather it implicates selection that favors any constellation of attentional, mnemonic, and sensorimotor biases that collectively aid acquisition, use, and transmission of language. Although this could conceivably consist of innate language-specific knowledge, Deacon (23, 27) argues that this is less likely than more general cognitive biases that facilitate reliable maintenance of this extrinsic niche. Baldwinian selection can only occur if there is a consistent and nondistributed genotype–phenotype relationship from person to person and from generation to generation, as well as a significant reproductive consequence of this specific linkage as opposed to others (25, 26). Because the particular way that a grammatical category relation or a syntactic operation is instantiated in a given language is arbitrary (e.g., a class of words, word order constraints, inflectional modifications, etc.), the evolvability of innate grammatical principles should be only slightly better than for innate words. Thus a recent study by Christiansen et al. (24) demonstrates that selection affecting the most generic and ubiquitous demands associated with language use, ac-

quisition, and transmission inevitably trumps the weak selection for arbitrarily instantiated language-specific features.

Therefore, although it seems beyond doubt that the human language capacity must have evolved due to extensive selection affecting multiple levels of adaptive mechanisms, both the form of the variant of natural selection that was involved and the nature of the cognitive capacity that it produced remain topics of intense debate in evolutionary biology. Whatever account is given, however, it must explain the evolution of the complex interdependence of the neurological, behavioral, and social transmission features of language. To the extent that we can identify generative biological processes that increase the probability of the expression of synergistic relationships among traits, then, these processes are likely to be relevant to language evolution. We turn to these next.

Evolution-Like Processes in Development

Understanding how and why natural selection produces complexity has been significantly advanced by recognizing how Darwinian-like processes that take place at other levels of development and scale contribute. One developmental mechanism that is particularly relevant to the evolution of cognitive complexity is the selection-like process that fine-tunes axonal connection patterns in the developing nervous system. The global organization of mammal brains exhibits a deep conservatism, with common epigenetic mechanisms responsible for their segmental organization and the determination of large-scale connection patterns between regions (29–31). But complementary to this underlying commonality of architecture generated in the early phases of embryogenesis, there is also a later plastic, and more-or-less "regressive" phase of brain development, that contributes to the variations on this general theme (32–36). The fine-tuning of neural circuitry to match specific body architecture and sensory specializations, and their variations within and between species, involves a sculpting logic that is loosely analogous to natural selection in a number of ways. The establishment of neural connections by axonal outgrowth and invasion initially involves a somewhat nonspecific phase where axonal guidance is largely controlled by highly conservative attraction, repulsion, and adhesion mechanisms, largely the result of local gene expression effects. This process appears to be fairly species-general, with many mechanisms shared by a wide range of vertebrates.

Although slight tweaks of this species-general brain architecture likely play important roles in producing the structural and functional differences of different species' brains, a significant contribution also comes from selection-like processes that incorporate both intra- and extraorganismic information into the fine-tuning of neural circuitry. The species-general global pattern of connectivity that is under strong but low-resolution genetic guidance becomes the scaffolding for subsequent connectional differentiation in response to signal-mediated activity-dependent competition for synaptic stability (37). These competitive interactions appear to follow a Hebbian signal-correlation logic that is characterized by the mnemonic "neurons that fire together wire together." In many systems, the competitive culling of connections is also correlated with neuronal apoptosis ("programmed" cell death). This process produces the fine-scale precision of connection patterns that match the neural populations and topographies of interdependent brain and peripheral structures.

This reflects one of life's general strategies for dealing with the problem of getting a vast array of organism features to achieve good functional integration with one another—effectively adapted to complement one another—with maximum flexibility and minimum design information. A precursor to this idea was proposed in the 1890s by the influential Darwinian and embryologist August Weismann, who is remembered mostly because of his success at repudiating the concept of Lamarckian inheritance. To provide an alternative explanation for features that Lamarckians had assumed would require a use-inheritance process, he suggested that there might be an *intraselection* process occurring in what amounts

[†]Two other theorists are credited with independently proposing the same theory in the same year: Conwy Lloyd Morgan (20) and Henry Fairfield Osborn (21, 22).

to the ecosystem of the body (38). Though differing from what Weissman originally intended, the axonal selection process is indeed a sort of intraorganismic selection process, although its logic differs from natural selection in one important respect: selection of this sort is confined to differential preservation only, not differential reproduction. In this respect, it is like one generation of the operation of natural selection. This more general way of characterizing the distinctive logic of natural selection was characterized by an early advocate of this generalization of Darwinism, Donald T. Campbell, with the phrase “blind variation with selective retention” (39).

This is relevant to the problem of evolvability. In general, the more highly complex, interconnected, and functionally integrated the system, the more likely it will be functionally degraded by structural variation. This is why no one imagines that computer design will be improved by randomly sampling alternative circuit plans. To maintain functional continuity despite local structural changes should require compensatory reorganization throughout. Thus if brain circuits were fully prespecified genetically, they would likely be too fragile to be evolvable.

The role that this intraselection process plays in the adaptive evolution of the brain is exemplified by the brain of the blind mole rat, *Spalax* (40). This fossorial species has vestigial eyes. In its brain, the lateral geniculate nucleus (the thalamic visual nucleus) is “invaded” during development by brainstem auditory and somatic projections that outcompete the sparse projections coming from the small retinas. The projections from the thalamus to the posterior cortex that in other mammals would subservise visual processing instead subserves somatic and auditory functions. Experimental manipulations in other species, in which projections from one sensory modality are reduced in early development, likewise exhibit analogous takeover effects (41, 42), and manipulations of the sensory periphery likewise demonstrate that intraselection adapts neural functional topography with respect to functional experience. This is a significant contribution to brain evolvability and a general mechanism available for natural selection to recruit. These mechanisms are almost certainly relevant to human brain evolution for language, especially considering that language is such a significant contributor to early experience.

This neuroepigenetic variant of selection logic is only one among many processes that might more generally be described as intraevolutionary mechanisms—i.e., intraorganismic morphogenetic processes that parallel attributes characteristic of phylogenetic evolution. Although they each differ in certain respects from natural selection, they all share certain attributes that distinguish them from “design” processes, analogous to the way that natural selection is distinguished from intelligent or end-directed design. First, they involve processes that produce functional integration and/or adaptation even though they are generated by mechanisms that are dissociated from this consequence. Second, they all involve the generation of redundant variant replicas of some prior form (gene, cell, connection, antibody, etc.) brought into interaction with each other and with an external context in a way that allows these differences to affect their subsequent distribution. And third, their preservation and expression are dependent on correlation with context. This highly abstracted analogy to Darwinian logic will be demonstrated by examples to follow, but it can be summarized as this: the replication, variation, and differential preservation that together characterize natural selection have their counterparts in the redundancy, degeneracy, and functional

interdependencies that characterize intraorganismic processes. This parallelism is summarized in Table 1.

These intraorganismic parallels to evolutionary processes can be generally distinguished with respect to the level at which selection acts and how this interacts with processes generating functional redundancy. All take advantage of the power of the replicative dynamic of life, expressed in growth and body maintenance as well as in reproduction, because of the redundancy that this produces.

Case 1. Internal Redundancy

The paradigm example of a replication–variation–selection dynamic occurring internal to the organism is gene duplication. This intragenomic duplication process has played a critical role in the evolution of organism complexity, and is widely accepted to be a fundamental source of functional synergies at all levels of the organism, from molecular complexes and their interactions to body appendages and their coordination (43–47). The Darwinian parallels of this intragenomic process are, however, seldom noted. In this process too, duplication allows variants to evolve, but largely because the presence of a redundant copy can relax selection that otherwise would tend to eliminate variant forms with mutations that alter critical functions. Where a redundant copy is not itself a source of maladaptation, single nucleotide substitutions and other noncatastrophic modifications to its sequence tend to progressively and incrementally degrade the functions of its protein product over evolutionary time.

Consider the well-documented case of the hemoglobins (48, 49). Spontaneous duplication of the ancestral hemoglobin gene into the alpha and beta forms allowed each to accumulate mutations that, while maintaining their oxygen-binding function, modified other features of tertiary structure. Independent variations in each form would originally have accumulated in the population, but sexual recombinations of different forms would have exposed any interaction effects between variants, increasing variants that in combination would have in some way augmented function. The one favorable interaction effect that ultimately evolved to fixation was a complementarity in tertiary shapes that increased the probability of the two variants binding to each other into a 2×2 tetrameric form with an improved oxygen-carrying capacity. This synergistic effect thus emerged from a duplication, independent variation, and eventual selection based on fitness to context (which in this case is the context consisting of the other hemoglobin variant).

In placental mammals the beta hemoglobin was further subject to multiple duplication mutations over the course of evolution. The resulting relaxation of selection has allowed two of these duplicates to degrade to pseudogene status. Four others, however, with slightly variant oxygen-binding characteristics, appear to have been coselected with respect to the different oxygenation demands of fetal life at different stages of gestation, with different variants expressed early and late in fetal development. This different sort of synergy—expressed diachronically rather than synchronically—was also facilitated by relaxed selection, and the way it increased the probability of interaction effects being expressed and thus becoming subject to selection, over and above the function of component genes.

The relaxation of selection that is created by the functional redundancy consequent to gene duplication enables what amounts to a random walk away from the gene’s antecedent function. But because a random walk produces incremental deviation, there is

Table 1. Parallels between evolution-like processes between and within organisms

Interorganism	Intraorganism
1. Reproduction and development	1. Duplication of structure and/or function
2. Divergence via mutation, recombination, and/or drift	2. Degeneracy and/or dedifferentiation
3. Environment-correlated preservation via superior fitness	3. Function-correlated preservation via complementation or synergy

a significant nonzero probability that one or more of the increasingly variant forms within a population of organisms will “wander” into a related interaction relationship with some duplicate counterpart, and again become subject to selection for any interactive deleterious or synergistic effects. It is no surprise, then, that gene families descended from a common ancestral gene often form synergistic functional complexes.

The logic of gene duplication is exactly inverted in one respect to that of natural selection. The relaxation of selection produced by internal redundancy reduces competitive elimination, and instead favors preservation of variant forms, thus increasing the random exploration of what might be called adjacent function space. As a result, it increases the probability of encountering both deleterious interactions and synergistic complementarities. Unlike axonal culling or the selective amplification of immune cell replication with respect to antigen presentation, this process occurs phylogenetically rather than ontogenetically, but the replication, variation, and context-dependent selection takes place within as well as between organisms.

This pattern of duplication, relaxation of selection, functional degradation, and the potential emergence of selection favoring new serendipitous synergistic interactions is replicated at many levels of organism complexity. For example, the duplication and differentiation of regulatory genes, such as the well-studied homeobox-containing genes that control segmental organization in insects and vertebrates via their regulation of the expression of a diverse range of other genes, enables duplication–degradation–complementation at the phenotypic level (50, 51). The generation of structural redundancy of body parts (e.g., limbs) via segmental duplication similarly relaxes selection on some with respect to others. Again, this increases the probability that random walk degradation will expose synergistic possibilities (e.g., of locomotor function) that will become subject to selective stabilization in their own right.

Case 2. External Redundancy

Functional duplication that has its origin external to the organism is analogous to gene duplication in influence, but can lead to very different consequences. Without the reliability of internal redundancy, irreversible degradation often follows and can lead to displacement of selection onto other loci that incidentally contribute some role in stabilizing access to the extrinsic source.

Consider the example of the loss of endogenous ascorbic acid (vitamin C) synthesis that has evolved in a few vertebrate lineages. Most vertebrates synthesize ascorbic acid endogenously, because of its important antioxidant functions, but anthropoid primates, fruit bats, guinea pigs, and many birds have lost this capacity (52). Among the primates, all prosimians except Tarsiers also synthesize ascorbic acid endogenously. We, along with other monkeys and apes, must regularly acquire vitamin C from dietary sources: principally fruit. And yet the human genome includes a pseudogene for the final enzyme in the ascorbic acid synthesis pathway: l-gulonolactone oxidase (GULO) (53). The human GULO gene (as a likely exemplar of its other anthropoid homologs) has accumulated many randomly distributed substitutions, deletions, and at least one major frame shift effect, which resulted in catastrophic loss of function (54).

Presumably, this drift toward degradation of function was a consequence of a change in diet of the ancestors of modern anthropoids to include significant and reliable quantities of fruit. Regular dietary substitution of ascorbic acid from fruit relaxed selection that would otherwise have regularly eliminated mutational variants with reduced ascorbic acid synthesis. Relaxation of this stabilizing selection allowed functional degradation of the GULO gene without negative reproductive consequences. But this loss of function resulted in the analog to a form of dietary addiction. Because this essential nutrient was only available extrinsically, selection to maintain its antioxidant function shifted to any sensory biases, behavioral tendencies, and digestive-metabolic mecha-

nisms that increased the probability of obtaining it. What was once selection focused on a single gene locus became fractionally distributed across a great many loci instead. One striking and plausible correlate is the evolution of three-pigment color vision in anthropoid primates, which coincidentally also involves gene duplication effects, the first of which appears to have occurred just before the divergence of Old and New World primates (55, 56).

Case 3. Global External Redundancy (e.g., Domestication)

In the rare cases where species enter domains with minimal direct competition (such as invasive founder species) or are otherwise minimally exposed to reproductive and survival limitations (e.g., domestication), the relaxation of selection this produces can result in global dedifferentiation effects. In such conditions, not only should we expect to see redistribution of functional determination, such as characterize cases of specific extrinsic redundancy, but it should be a more or less generalized effect. This should be particularly well exemplified in long-domesticated species such as the domestic dog.

An example of domestication that might shed light on the language origins issue involves domestication of a songbird known as the White-Backed Munia (57, 58). Its domesticated cousin is known as the Bengalese Finch, which has been bred for coloration in Japan for roughly 250 years. Interestingly, although as far as is known, it was never specifically bred for singing ability (and does not have a particularly sonorous song), the Bengalese Finch has a very different singing ability than its wild cousin. Bengalese Finches acquire their songs via social learning by copying a particular adult singer or singers. As a result, their songs are highly variable within and between individuals. In contrast, the White-Backed Munia does not learn its song from others and has an autonomously developed and highly rigid song.

Birdsong, like other forms of display complexity, are generally assumed to be the result of sexual selection, where it contributes to competition for mates, territory, nest sites, etc. In this case, however, it appears to have complexified in conditions where selection on song function has been completely relaxed.[‡] Variability can simply be a correlate of degradation of control, and this would indeed be an expected consequence of relaxation of selection; however, the shift from autonomously developed to socially acquired song requires a bit more explanation. In addition, socially acquired song requires the contribution of a significantly larger number of forebrain nuclei and their interconnections than does the production of a mostly innately prespecified song (59). This difference also distinguishes the Bengalese Finch from the White-Backed Munia.

Generally, it is assumed that an increase in behavioral complexity and flexibility and an increase in the complexity of neural interactions that support it can only have come about due to intense natural or sexual selection. In this case, however, increased complexity appears to have arisen in the context of global relaxation of selection, and in a remarkably brief period. This apparent paradox can be resolved if we understand the transition in terms of the dedifferentiation and redistribution effects of relaxed selection.

Although data are not currently available to delineate what mechanism generated this difference, its association with an apparent global relaxation of selection suggests the following hypothesis.

By removing the stabilizing effects of natural and sexual selection on song production, the almost exclusive control of song structure by a forebrain nucleus designated RA[§] degraded, as genes maintaining this behavioral template acquired degrading

[‡]Although it is possible that song complexity was inadvertently selected either by unconscious bias during breeding or because of linkage, epistatic, or pleiotropic association with the genetics of coloration, no evidence for such a coupling exists. And in addition, each of these theories makes unusual assumptions that are not required for the relaxed selection account. Genetic analysis will be required to ultimately choose between these mechanisms.

[§]Robust nucleus of the Archistriatum.

mutations that were not eliminated by selection. As constraints on song generation degraded with prolonged domestication, other neural systems that previously were too weak to have an influence on song structure could now have an effect. These include systems involved in motor learning, conditionally modifiable behaviors, and auditory learning. Because sensory and motor biases can be significantly affected by experience, song structure could also become increasingly subject to auditory experience and the influence of social stimuli. In this way, additional neural circuit involvement and the increased importance of social transmission in the determination of song structure can be reflections of functional dedifferentiation, and yet can also be sources of serendipitous synergistic effects as well. The result is a tendency to shift control of a previously innate and localized function onto a distributed array of systems that each now only fractionally influence that function. This effectively offloads a significant degree of genetic control onto epigenetic processes, and because of their openness to experiential modification, it increasingly opens the door to the influence of social transmission (60).

There are a number of features that distinguish the neurology of linguistic communication from that of the major forms of vocal communication in other primates (and mammals in general) that appear to have parallels in the Finch/Munia case. These include (i) a significant decrease in the specific arousal-coupling of vocal behaviors, (ii) minimization of constraint on the ordering and combinations of vocal sounds, (iii) reduction, simplification of the innate call repertoire, (iv) subordination of innate call features to a secondary role in emotional tone expression via speech prosody, (v) a significantly increased role of auditory learning via social transmission, (vi) widely distributed synergistic forebrain control of language compared with highly localized subcortical control of innate vocalizations, and, of course, (vii) an increased social-cognitive regulation of the function of vocal communication (60).

This raises an obvious question: Could humans be a self-domesticated species—i.e., a degenerate ape? The Munia/Finch analogy suggests that genetic dedifferentiation affecting the nervous system may have contributed to functional complexity in human language evolution. Has there been more widespread degeneration as well? If so, it might help explain the extensive human cognitive–social–emotional flexibility compared with other mammalian species. Could human mental plasticity, cultural variability, aesthetic and religious sensibilities, and susceptibility to social control and conformity be an expression of cognitive–emotional dedifferentiation?

Putting Humpty Dumpty Together Again

This exploration of intraorganism parallels to evolutionary processes of selection and drift has highlighted a number of mechanisms by which remarkably complex synergistic relationships can emerge serendipitously in the course of evolution. These processes are not exclusive of the effects of natural and sexual selection, and in many ways provide auxiliary sources of complex synergy subject to these Darwinian processes. They are almost certainly crucial to the evolvability of highly complex synergistic adaptations, such as human language. Recognition of the potential contributions of each of these processes to evolvability should warn against monolithic natural selection accounts of language evolution that ignore the contributions of these interlinked levels of selection and drift processes.

But language evolution includes one additional twist that may in fact mitigate some fraction of what biological evolutionary mechanisms must explain. Language itself exhibits an evolutionary dynamic that proceeds irrespective of human biological evolution. Moreover, it occurs at a rate that is probably many orders of magnitude faster than biological evolution and is subject to selective influences that are probably quite alien from any that affect human brains or bodies. Darwin recognized this analogical process, although he did not comment on its implications for human brain evolution.

“A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand, and they owe their success to their own inherent virtue” (ref. 11, p. 91).

The environment that is the source of selection affecting the reproduction and selective elimination of language features is human cognitive limitation and communicative requirements. For this reason, a given language should reflect selection favoring learnability, early acquisition, and ease of use concerning which features are retained or lost over the course of its historical change. In this respect it is an oversimplification to expect that all of the universal design features of language require a biological evolutionary account. So as brains have adapted to the special demands of language processing over hundreds of thousands of years, languages have been adapting to the limitations of those brains at the same time, and a hundred times faster (27). This means that brain functions selected for the special cognitive, perception, and production demands of language will reflect only the most persistent and invariant demands of this highly variable linguistic niche. This is another reason to expect that the synergistic constellation of human brain adaptations to language will not include specific grammatical content, and to suspect that much of the rich functional organization of any language is subject to influences on this extragenomic form of evolution. In other words, the differential reproduction of language structures through history will be dependent on the fidelity and fecundity of their transmission. Not only will this process be subject to selection with respect to semiotic and pragmatic demands of symbolic communication, it will also favor structures that are more easily acquired by immature brains undergoing activity-dependent intraselection of neural circuitry. Indeed, just as evolvability is aided by evolution-like processes involved in ontogenesis, we should expect that the social evolution of language should itself exhibit analogous processes due to redundancy, degeneracy, and functional interdependency.

Language is too complex and systematic, and our capacity to acquire it is too facile, to be adequately explained by cultural use and general learning alone. But the process of evolution is too convoluted and adventitious to have produced this complex phenomenon by lucky mutation or the genetic internalization of language behavior. These metaphors are more suited to the analysis of a designed artifact. The robusticity of the language acquisition process, the deep integration of language and human cognition, and the involvement and synergistic interaction of widespread and diverse brain systems in language processes together imply that there has been long-term adaptation involving a very broad suite of genetic loci and the involvement of many levels of intraevolutionary mechanisms. We are more likely to succeed at solving this mystery if we approach it with the expectation that nature produces her most complex works by a logic that is vastly more subtle, and entirely unlike the methods of a watchmaker or computer scientist.

1. Darwin C (1838) E Notebook. Available at <http://darwin-online.org.uk/content/frameset?viewtype=side&itemID=CUL-DAR124-&pageseq=50>. Accessed January 27, 2010.
2. Darwin C (1859) *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London).
3. MacKenzie RB (1868) The Darwinian Theory of the Transmutation of Species Examined (published anonymously “by a graduate of the University of Cambridge”) (Nisbet, London) [Quoted in a review, *Athenaeum*, no. 2102, February 8].
4. Wallace AR (1869) Sir Charles Lyell on geological climates and the origin of species. *Quarterly Review* 126:359–394.

5. Lyell C (1863) *Geological Evidences of the Antiquity of Man* (John Murray, London).
6. Bynum WF (1984) Charles Lyell's Antiquity of Man and its critics. *J Hist Biol* 17:153–187.
7. Chomsky N (1986) *Knowledge of Language: Its Nature, Origin and Use* (Praeger, Santa Barbara, CA).
8. Chomsky N (2005) Three factors in language design. *Ling Inq* 36:1–22.
9. Pinker S (1994) *The Language Instinct: How the Mind Creates Language* (William Morrow, New York).
10. Darwin C (1860) Letter 2743—Darwin, C. R. to Gray, Asa, 3 Apr 1860. Available at <http://www.darwinproject.ac.uk/entry-2743>. Accessed January 27, 2010.

11. Darwin C (1871) *The Descent of Man and Selection in Relation to Sex* (John Murray, London).
12. Wallace AR (1870) *Contributions to the Theory of Natural Selection* (Macmillan, London), 2nd Ed.
13. Trivers RL (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man 1871-1971*, ed Campbell B (Aldine, Chicago), pp 136-179.
14. Miller G (1999) Sexual selection for cultural displays. *The Evolution of Culture*, eds Dunbar R, Knight C, Power C (Edinburgh Univ Press, Edinburgh), pp 71-91.
15. Burling R (2005) *The Talking Ape. How Language Evolved* (Oxford Univ Press, Oxford).
16. Locke JL, Bogin B (2006) Language and life history: A new perspective on the development and evolution of human language. *Behav Brain Sci* 29:259-280, discussion 280-325.
17. Mellars P (1996) The emergence of biologically modern populations in Europe: A social and cognitive revolution?. *The Evolution of Social Behaviour Patterns in Primates and Man*, eds Runciman G, Maynard-Smith J (British Academy, London), pp 179-201.
18. Klein R (2002) *The Dawn of Human Culture* (Wiley, New York).
19. Baldwin J (1896) A new factor in evolution. *Am Nat* 30:441-451, 536-553.
20. Morgan CL (1896) On modification and variation. *Science* 4:733-740.
21. Osborn HF (1896) Ontogenic and phylogenic variation. *Science* 4:786-789.
22. Osborn HF (1897) The limits of organic selection. *Am Nat* 31:944-951.
23. Deacon TW (2003) Multilevel selection in a complex adaptive system: The problem of language origins. *Evolution and Learning: The Baldwin Effect Reconsidered*, eds Weber B, Depew D (MIT Press, Cambridge, MA), pp 81-106.
24. Christiansen MH, Reali F, Chater N (2006) The Baldwin effect works for functional, but not arbitrary, features of language. *Proceedings of the Sixth International Conference on the Evolution of Language*, eds Cangelosi A, Smith A, Smith K (World Scientific, London), pp 27-34.
25. Federici D (2003) Culture and the Baldwin effect. *Advances in Artificial Life: 7th European Conference, ECAL 2003, Dortmund, Germany, September 2003 Proceedings*, eds Banzhaf W, Christaller Th, Dittrich P, Kim JT, Ziegler J (Springer, Berlin), pp 309-318.
26. Yamauchi H (2007) How does Niche construction reverse the Baldwin effect?. *Advances in Artificial Life: 9th European Conference, ECAL 2007, Lisbon, Portugal, September 2007 Proceedings*, eds Costa FA, Rocha LM, Costa E, Inman H, Coutinho A (Springer, Berlin), pp 315-324.
27. Deacon TW (1997) *The Symbolic Species: The Coevolution of Language and the Brain* (Norton, New York).
28. Odling-Smee FJ, Laland KN, Feldman MW (2003) *Niche Construction: The Neglected Process in Evolution* (Princeton Univ Press, Princeton, NJ).
29. Striedter GF (1997) The telencephalon of tetrapods in evolution. *Brain Behav Evol* 49: 179-213.
30. O'Leary DDM, Nakagawa Y (2002) Patterning centers, regulatory genes and extrinsic mechanisms controlling arealization of the neocortex. *Curr Opin Neurobiol* 12:14-25.
31. Mallamaci A, Stoykova A (2006) Gene networks controlling early cerebral cortex arealization. *Eur J Neurosci* 23:847-856.
32. Purves D, Lichtman JW (1980) Elimination of synapses in the developing nervous system. *Science* 210:153-157.
33. Cowan WM, Fawcett JW, O'Leary DDM, Stanfield BB (1984) Regressive events in neurogenesis. *Science* 255:1258-1265.
34. Wilczynski W (1984) Central neural systems subserving a homoplasous periphery. *Am Zool* 24:755-763.
35. Finlay BL, Wikler KC, Sengelaub DR (1987) Regressive events in brain development and scenarios for vertebrate brain evolution. *Brain Behav Evol* 30:102-117.
36. Deacon TW (1990) Rethinking mammalian brain evolution. *Am Zool* 30:629-705.
37. Krubitzer L, Kaas J (2005) The evolution of the neocortex in mammals: How is phenotypic diversity generated? *Curr Opin Neurobiol* 15:444-453.
38. Weismann A (1894) The effect of external influences upon development. *The Romanes Lecture, 1894* (H. Frowde, London).
39. Campbell DT (1965) Variation and selective retention in socio-cultural evolution. *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory*, eds Barringer H, Blanksten G, Mack R (Schenkman, Cambridge, MA), pp 19-49.
40. Doron N, Wollberg Z (1994) Cross-modal neuroplasticity in the blind mole rat *Spalax ehrenbergi*: A WGA-HRP tracing study. *Neuroreport* 5:2697-2701.
41. Frost DO (1981) Orderly anomalous retinal projections to the medial geniculate, ventrobasal, and lateral posterior nuclei of the hamster. *J Comp Neurol* 203:227-256.
42. Sur M, Garraghty PE, Roe AW (1988) Experimentally induced visual projections into auditory thalamus and cortex. *Science* 242:1437-1441.
43. Ohno S (1970) *Evolution by Gene Duplication* (Springer, Berlin).
44. Li WH (1983) Evolution of duplicate genes and pseudogenes. *Evolution of Genes and Proteins*, eds Nei M, Koehn R (Sinauer, Sunderland, MA), pp 14-37.
45. Ohta T (1994) Further examples of evolution by gene duplication revealed through DNA sequence comparisons. *Genetics* 138:1331-1337.
46. Walsh JB (1995) How often do duplicated genes evolve new functions? *Genetics* 139: 421-428.
47. Zhang J (2003) Evolution by gene duplication: An update. *Trends Ecol Evol* 18: 292-298.
48. Goodman M, Czelusniak J, Koop BF, Tagle DA, Slightom JL (1987) Globins: A case study in molecular phylogeny. *Cold Spring Harb Symp Quant Biol* 52:875-890.
49. Hardison R (1999) The evolution of hemoglobin. *Am Sci* 87:126-137.
50. Garcia-Fernández J (2005) The genesis and evolution of homeobox gene clusters. *Nat Rev Genet* 6:881-892.
51. Martindale MQ (2005) The evolution of metazoan axial properties. *Nat Rev Genet* 6: 917-927.
52. Chatterjee IB (1973) Evolution and the biosynthesis of ascorbic acid. *Science* 182: 1271-1272.
53. Nishikimi M, Fukuyama R, Minoshima S, Shimizu N, Yagi K (1994) Cloning and chromosomal mapping of the human nonfunctional gene for L-gulonono-gamma-lactone oxidase, the enzyme for L-ascorbic acid biosynthesis missing in man. *J Biol Chem* 269:13685-13688.
54. Ohta Y, Nishikimi M (1999) Random nucleotide substitutions in primate nonfunctional gene for L-gulonono-gamma-lactone oxidase, the missing enzyme in L-ascorbic acid biosynthesis. *Biochim Biophys Acta* 1472:408-411.
55. Shyue S-K, et al. (1995) Adaptive evolution of color vision genes in higher primates. *Science* 269:1265-1267.
56. Nei M, Zhang J, Yokoyama S (1997) Color vision of ancestral organisms of higher primates. *Mol Biol Evol* 14:611-618.
57. Honda E, Okanoya K (1999) Acoustical and syntactical comparisons between songs of the white-backed munia (*Lonchura striata*) and its domesticated strain, the Bengalese finch (*Lonchura striata var. domestica*). *Zool Sci* 16:319-326.
58. Okanoya K (2004) The Bengalese finch: A window on the behavioral neurobiology of birdsong syntax. *Ann N Y Acad Sci* 1016:724-735.
59. Jarvis ED (2004) Learned birdsong and the neurobiology of human language. *Proc Natl Acad Sci USA* 1016:749-777.
60. Deacon TW (2009) Relaxed selection and the role of epigenesis in the evolution of language. *Oxford Handbook of Developmental Behavioral Neuroscience*, eds Blumberg MS, Freeman JH, Robinson SR (Oxford Univ Press, New York), pp 730-752.