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Di Sciullo, A.M.; Piattelli-Palmarini, M.; Wexler, K.; Berwick, R.C.; Boeckx, C.; Jenkins, L.; ... ; Bever, T.G.

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The Biological Nature of Human Language

Anna Maria Di Sciullo, Massimo Piattelli-Palmarini, Kenneth Wexler, Robert C. Berwick, Cedric Boeckx, Lyle Jenkins, Juan Uriagereka, Karin Stromswold, Lisa Lai-Shen Cheng, Heidi Harley, Andrew Wedel, James McGilvray, Elly van Gelderen
& Thomas G. Bever

Biolinguistics aims to shed light on the specifically *biological* nature of human language, focusing on five foundational questions: (1) What are the properties of the language phenotype? (2) How does language ability grow and mature in individuals? (3) How is language put to use? (4) How is language implemented in the brain? (5) What evolutionary processes led to the emergence of language? These foundational questions are used here to frame a discussion of important issues in the study of language, exploring whether our linguistic capacity is the result of direct selective pressure or due to developmental or biophysical constraints, and assessing whether the neural/computational components entering into language are unique to human language or shared with other cognitive systems, leading to a discussion of advances in theoretical linguistics, psycholinguistics, comparative animal behavior and psychology, genetics/genomics, disciplines that can now place these longstanding questions in a new light, while raising challenges for future research.

Keywords: language development and genetics; linguistic competence in a comparative ethological context; linguistic theory; neurology of language and the genome

1. Introduction: Background and Overview

This short article brings together for biologists and linguists recent hypotheses, studies, and results on the human faculty of language stemming from the Biolinguistic Program. It is not intended to cover in full all current research relating biology and language; nor could it hope to do so. Rather, the specific topics discussed here may be taken as illustrating just some of the current lively

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research in this field.

The modern Biolinguistic Program initially grew out of collaboration between biologists and linguists in the late 1950s and early 1960s, initially Eric Lenneberg and Noam Chomsky, and later Salvador Luria among others, epitomized in Lenneberg's *Biological Foundations of Language* (Lenneberg 1967). A 1974 international meeting at MIT called *Biolinguistics* by its organizer, Massimo Piattelli-Palmarini, propelled it further. More recently, books and papers surveying the field and proposing new directions have been published (e.g., Jenkins 2000, 2004; but for a very different approach, see Givón 2002); and conferences have been organized worldwide, coupled with the 2006 launch of this journal, *Biolinguistics*, and the foundation of an international network on biolinguistics in 2007 (www.biolinguistics.uqam.ca; for an overview, see the forum contribution to this issue, Di Sciullo 2010).

A variety of contemporary theories and research programs provide a way to relate biology and language. For example, the 'Minimalist Program' (Chomsky 1995 and related works¹) provides a methodology to explain linguistic phenomena with minimal theoretical apparatus, attempting to make contact with biology, physics, psychology, and computational neuroscience.² The Minimalist Program in the broad sense, including the insights discovered in earlier work, such as the Principles-and-Parameters model (Chomsky 1981) and the formal approach to syntactic structure (Chomsky 1956), has been very successful in shedding light on a number of the questions raised by Biolinguistics. This is not to say, for example, that Minimalism predicts the *FOXP2* gene in language or the organization of the language areas in the brain.³ Given our current understanding, no research program or theory can do this. For the moment, it suffices that a linguistic research program should suggest productive avenues to explore in order to illuminate the biological nature of language.

The Biolinguistic Program proceeds by trying to answer (classical) questions about the mechanism, the development, and the evolution of language. *What is knowledge of language? How does language develop in the child? How does language evolve in the species?* Each can be studied at different levels. Knowledge of language can be studied at an abstract, top level, by positing a 'faculty of language' that includes a generative grammar with various properties, including recursion, structure-dependence, symmetrical and asymmetrical properties, and the like. Knowledge of language can also be studied at the neural level, using tools of brain area mapping (e.g., Broca/Wernicke areas, noun/verb regions,

¹ See, e.g. (in alphabetical order), Boeckx (2006, 2008), Chomsky (2000, 2001, 2005, 2009a, 2009b), Di Sciullo (2003a, 2003b, 2005, in press), Hinzen (in press, to appear), Lasnik (1999, 2002, 2003, in press a, b), Martin & Uriagereka (2000), McGilvray (2005, 2006), Uriagereka (1998, 1999), and Uriagereka & Boeckx (2007).

² See, among other works (in alphabetical order again), Belletti & Rizzi (2002), Berwick (in press), Berwick & Chomsky (in press), Berwick & Weinberg (1986), Boeckx & Piattelli-Palmarini (2005), and Di Sciullo & Boeckx (in press).

³ We will use the following nomenclature for *FOXP2* (see also <http://biology.pomona.edu/fox>): "Briefly, nucleotide sequences are italicized whereas proteins are not. Human forms are capitalized (e.g. *FOXP2* protein), murine forms are in lowercase (e.g. *Foxp2*), and those of other species, such as the zebra finch, are in uppercase and lowercase (e.g. *FoxP2*)" (Teramitsu *et al.* 2004: 3152).

etc.), imaging, probes, and so forth. Ultimately, we want to link grammars to the brain, but at this stage we do not expect to be able to predict properties of neural organization from properties of grammar. But if we find that, for example, certain areas are active for verbs and others for nouns, then this is consistent with a grammatical theory with a verb/noun distinction, but not with one that has no such distinction. Other topics such as brain lateralization and handedness can also be studied at multiple levels (Bever *et al.* 1989, Geschwind & Galaburda 1985). Similar remarks apply to sign languages.

Similarly, the Biolinguistic Program can study the development of language at an abstract level, positing a Universal Grammar to account for both universal properties and language variation (say, by adopting parameters along the lines of Chomsky's Principles-and-Parameters program, together with a probabilistic model as proposed by Yang (2002), or Kayne's (2005) micro-parameters in comparative linguistics. Alternatively, one can study this area more concretely by looking at the developmental trajectories of actual children (Wexler 2003). In just the same way, critical periods can be studied abstractly (Stromswold 2005) or concretely by looking at genetic programs in other critical period systems. In some cases one can even investigate at the level of single genes, as with *FOXP2*, where one can link the abstract patient behavior (verbal dyspraxia) with genetic mutations (Gopnik 1990, Vargha-Khadem *et al.* 1995). We can do the same with other genetic disorders—DNA duplication, chromosome disorders, language in Williams Syndrome, dyslexia, etc. Finally, the Biolinguistics Program can address the question of the evolution of language (as well as language change) at the abstract level by computer simulation (Niyogi & Berwick 1997, 2009, Nowak *et al.* 2002, Niyogi 2006,) or via cross-species behavioral studies (starlings, cotton-top tamarins, etc.). Again at a more concrete level, one can carry out cross-species comparisons of *FOXP2* and of other genes affecting language. Finally, questions as to why the language faculty has certain properties and not others can be linked to all three levels above, and might include memory constraints on parsing, economy conditions, (a)symmetry, or—more concretely—wiring minimization.

Crucially, the Biolinguistic Program explicitly factors the 'faculty of language' into three components consonant with biology generally—language's genetic endowment, 'Universal Grammar', environmental experience, and biophysical principles that are language-independent (Chomsky 2005, and related works).⁴ It connects historically with a line of inquiry attentive to the 'laws of form', that is, to the topological, computational and self-organizational invariants of life forms, going back to D'Arcy Thompson and Turing.

A major aim of the Biolinguistic Program has been to explain why Universal Grammar, extracted from commonalities across languages, is what it is and not something else. This basic question leads to an investigation of what the genome specifies that is particular to language, and raises the possibility that this genetic endowment specifies only a few, basic computational features. This approach has already led to two empirical benefits for research. First, by specifying

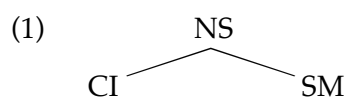
⁴ See, again in alphabetical order, Berwick (in press), Chomsky (2009a, 2009b), Di Sciullo (2007, in press), Jenkins (in press), Lasnik (in press), Medeiros (2008), Piattelli-Palmarini & Uriagereka (2004, 2005, 2008, in press), Piattelli-Palmarini *et al.* (2009), Uriagereka (in press).

a relatively compact set of computational principles, it enables a more direct link to animal behavior and evolutionary analysis than previously considered. This broader comparative approach enables a more systematic exploration of the components of the language faculty that are shared with other animals and other domains of human knowledge (the ‘broad’ faculty of language) and those that are unique to humans and language (the ‘narrow’ faculty of language) (Hauser *et al.* 2002). Second, it is now possible to integrate our understanding of how cognitive systems of learning and use constrain language universals with a general theory that spans biology and formal linguistics (e.g., Miller & Chomsky 1963, Bever 1970, Wexler & Culicover 1980).

We begin by providing a brief synopsis of minimalist proposals about the faculty of language and their import for Biolinguistics. We then turn to four sections that showcase discoveries that are consonant with minimalist proposals and that contribute to our understanding of the biological basis of language. First, we discuss recent findings on the acquisition of formal grammars by monkeys and other non-human species. We note that while there is also extensive work in aphasia and brain imaging, we have chosen to single out these cross-species analyses because they aim to provide experimental results on the human specific properties of the faculty of language. Second, in the area of language acquisition and child language disorders, we focus on tense and finiteness. Here too, whereas much current work is devoted to other linguistic aspects, such as difficulties in sentence structure and movement, the results of the study on tense and finiteness relate to the hypothesized properties of the faculty of language, including the asymmetry of (morpho-syntactic) features/projections. These studies also lead to promising genetic correlates. Third, we review recent advances in the genetics of language, with special emphasis on *FOXP2*. Finally, we turn to results on naming and dextrality/sinistrality (handedness) as they relate to the minimal assumptions about the faculty of language and lead to further inquiry in the relation between language and biology/genetics. Once again, there has been extensive work on anomia and its lexical basis, as well as syntactic impairments in aphasia, that are relevant to the discussion on whether syntax and the lexicon have different neurological foundations and which brain areas might be correlated with certain linguistic functions, but we have chosen to highlight the particular case of handedness as a ‘case study’. We conclude with a discussion of the promise of the Biolinguistic Program, as well as challenges for the future.

2. Theoretical Linguistics and Biolinguistics

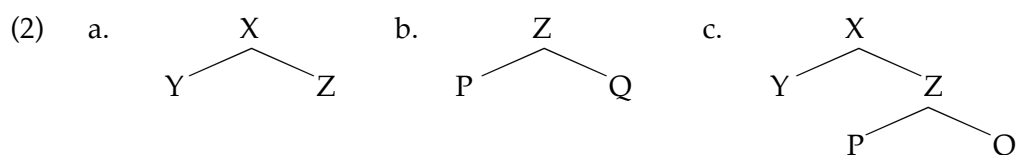
The configuration in (1) represents a minimalist proposal for the skeletal architecture of the human faculty of language, with a schema familiar to biologists as a framework for modeling other complex processes. It is the bare bones of our core linguistic apparatus.



This simple machinery produces a potential infinity of corresponding pairs of sounds and meanings. These paired instruction/information sets are passed on to and then interpreted by separate systems, external to the core computational system. The first is the Sensory-Motor system (SM): It satisfies the biological requirements imposed on the production and the perception of language (auditory in spoken languages, visual in sign languages). The biological requirements correspond to the structure and function of the auditory system in perception and to those of the vocal tract and articulatory apparatus in production. The second is the Conceptual-Intentional system (CI): It satisfies the biological requirements involved in interpretation, reasoning and inference, internal to the brain's other cognitive functions (Chomsky 1995, 2005). Adopting this division represented in (1) reduces to a minimum the parts of this architecture that are particular to human language, as opposed to more general kinds of biological computations. Crucially, like all biological machinery, (1) has only finite computational power, but must still produce an infinity of possible sound-meaning pairs, in Humboldt's famous phrase making "infinite use of finite means". This is the basic function of the narrow faculty of language, solving its core biological 'design problem', producing what is called 'narrow syntax' (NS). Conjecturing that (1) may be reduced to such a minimum is a strong claim about what the human genome specifies as the unique core of universal grammar. If this hypothesis is correct, then this language-specific genomic component is optimal in the sense that it is sufficient to solve the core system 'design' problem and no more. To draw an analogy to an example familiar to biologists, just as the human genome (with only about 24,000 genes) cannot and need not encode the precise neuron-to-neuron wiring of the brain (Cherniak *et al.* 2004), NS need not specify that spoken language must be produced according to the word-order rules of each particular language. There are solid grounds to suppose that word-order constraints are implicitly imposed by a language community from a biologically limited set of possibilities and by physical constraints on the articulatory system—we cannot say two things at once. In this way, what must be specified by the genome for NS is held to a bare minimum.

What remains? Sentences are obviously quite different from mere lists of words. While linguistic researchers often disagree on the details, they largely concur that the constituents of sentences are hierarchically structured phrases, themselves consisting of smaller units, commonly referred to as words, with their own internal morphological structure. In current computational theory, there is but one way to construct such an infinite variety of hierarchical structures using a finite set of elements, and that is via a recursive operator that combines parts together into new, larger wholes: Larger components are built from smaller parts. The elements of a sentence are combined by a local operation that connects components immediately adjacent in the hierarchy. The structures in (2) outline the simplest form of this operation. Characteristically, each sub-hierarchy is composed of a tree with a category node that dominates two categorized branches. A sub-hierarchy can be merged with another when the category at the top of one sub-tree matches one of the bottom branches of another, as shown. This operation can then apply again to its own output, building up more complex hierarchies, yielding an infinity of outcomes—sentences may contain other sentences, and

these in turn other sentences. In the Minimalist Program, this constructive operation is called ‘Merge’: This term is intuitively based on the fact that it connects two ‘sisters’ at the same hierarchical level, and then these together, as a unit, to the immediate higher node in the hierarchy, and then again and again to produce a more complex hierarchy. Many other linguistic traditions adopt principles similar in spirit, since there must be some means of solving the combinatory problem such that a finite system yields a potentially infinite output.⁵



Thus a central goal of the Biolinguistic Program is to characterize the biological properties of this recursive operator, beginning with its abstract properties, ultimately arriving at its concrete biological instantiation.⁶ To be sure, at this stage we know very little about how recursive computation is actually implemented in the brain. But at an abstract level, we know that Merge must have properties beyond recursion, since recursion alone is a generic property of any infinite output system, including mathematics and music. In particular, Merge must also be asymmetric in singling out one of the two initial elements (sisters) it operates on instead of another, for example, either always the left member of a tree like that in (2a), Y, or the right member, Z. Otherwise, all linguistic elements would be treated identically and there would be no differentiated structure in words, phrases, sentences, or anywhere else. In addition, Merge must be asymmetric in selecting the elements to which it applies. The sets of features of these elements must be in a superset/subset relation otherwise it would not be possible to satisfy their morpho-syntactic features. Thus, verbal inflection features, such as Tense, combine with verbal elements/projections; they do not combine with nominal elements/projections. The feature asymmetry stemming from the dynamics of Merge could be specific to the human language faculty. If so we would not expect to find manifestations of feature asymmetry in non-human primates and in other animals (see section 3). We would however expect the ability to compute feature asymmetry to be affected in specific language impairment (see section 5). It might be the case that the asymmetry of Merge and the hierarchical structures it derives is rooted in biology.

This is reminiscent of the way that asymmetry in developmental gradients derives structure in embryogenesis, or asymmetry in cell–cell adhesion or contractility generates mechanical forces that can be deployed combinatorially, developing a broad range of epithelial tissue types in morphogenesis (Montell 2008).⁷ This is also conceptually and computationally similar to the current

⁵ This problem is also addressed in frameworks other than Minimalism, such as Categorical Grammar, going back to Ajdukiewicz (1935), Bar-Hillel (1953), and Lambek’s (1958) seminal work, modeling the combinatory possibilities of the syntax of human languages.

⁶ See Hauser *et al.* (2002) on recursion, as a property of the language faculty, and Fitch (2010) on the importance of this notion for biolinguistics.

⁷ See also Boeckx (2006), Chomsky (1995, 2005), Di Sciullo (2003a, 2003b, 2005, in press), Di Sciullo & Isac (2008a, 2008b), Gelderen (2004, 2008), Hinzen (in press), Kayne (1994, 2002, in

inquiry into evolution and development (the ‘evo–devo’ theory of evolution) which underlies recent biological explanations of how the same battery of genes engenders a variety of life forms by small changes in the regulation of their timing and rate of expression. As with the morphological segmentation of body plans, the minute factors that produce repeated breaks in symmetry mold language’s shape in sometimes surprising ways. This is linguistic science’s own twist on the combinatorial power of simple units, explaining the diversity of languages, analogous to the biological processes that produce, in Darwin’s famous expression, “endless forms most beautiful” (Raff 1996, Jenkins 2000, Carroll *et al.* 2001, Carroll 2005).

3. Linguistic Competence in a Comparative, Ethological Context

Recent work on the evolution of language has turned from looking strictly at communication, to exploring the similarities and differences between humans and animals with respect to computational competence. This new angle has opened the door to exploring the capacity of animals to extract artificial grammars that represent the building blocks of linguistic syntax. This work suggests the novel possibility that humans share with animals some of this core foundation, but uniquely evolved the capacity to interface syntactic structures with semantic and phonological representations. In this way, experimental work with non-human primates provides data that can be used to identify the commonalities among human and animal languages.

Several studies build on this idea, using the formal approach to syntactic structures laid out by Chomsky (1956)—the formal hierarchy of rules and regularities—together with experimental work in artificial language learning. This research isolates specific kinds of linguistic computation that are most relevant to acquisition, including problems of segmentation, the extraction of algebraic rules, the relationship between types and tokens, and the relationships between abstract variables. For example, infants can use transitional probabilities to segment a continuous stream of speech; corresponding studies of rats and tamarin monkeys have provided parallel evidence. Adult humans and infants can extract abstract rules of the form AAB, ABA, and ABB; corresponding studies with rats and monkeys show similar abilities. Tamarin monkeys and starlings can recognize the strings generated by a grammar that places symbols in a simple line like beads on a string (patterns in the form $(AB)^n$). It has been argued that starlings reveal suggestive abilities—after a training that consists of several thousands of repetitions—at recognizing the strings of the next order of grammatical complexity generated by a grammar that ‘nests’ or embeds matching words or symbols hierarchically (patterns in the form (AB) , $(A(AB)B)$, $(A(A(AB)B)B)$, ..., $A^n B^n$) (Fitch & Hauser 2004, Gentner *et al.* 2006). More recently, such results have been called into question by more careful experimental tests with zebra finches suggesting that non-nesting rules alone suffice to account for

press), Langendoen (2003), Moro (2000, 2008), and Zwart (2006), for example, on the role of asymmetry and symmetry-breaking in the derivation of linguistic expressions.

the results (van Heijningen *et al.* 2009). Additional evidence of successful discrimination among tokens based on a particular rule leaves open alternative solution strategies. For example, strings of the form A^nB^n could be recognized by computing the hierarchy and embeddedness of AB pairs or simply by counting and checking for an equal number of A's and B's. While preliminary results are already available (see Figure 1, Friederici 2009), further work is necessary to understand the formal properties of animal computations and how they differ from the ones derived by human computation (Merge).⁸ More interesting artificial language paradigms could be tested to see whether tamarin monkeys and other animals can generate/recognize asymmetric relations, be they featural or hierarchical. For example, while humans compute indirect recursion, for example, *the queen's garden's roses, the cat on the tree in the garden*, experimental tests with animals using artificial language paradigms expressing left and right indirect recursion asymmetries, for example, AC BC D, where there is a different number of A's and B's and where C would stand for a functional category/ projection such as the possessive 's or a preposition in the previous examples from English, could be telling about the kind of complexity and asymmetric relations that can be computed by animals. There is much to be done in this area, as, to start with, it is unclear whether, given a set of elements {A, B, C}, animals may generate/recognize asymmetric relations, for example, AB BC AC or CB, CA BA, and so on, as opposed to symmetric ones, for example, AB BA AC CA BC CB.⁹ In any case, and notwithstanding the difficulties encountered to test the underlying computations in animals as well as in humans, this kind of work is likely to shed light on the species-specific computational machinery behind human language, by exploring the similarities and the differences with animal computation.

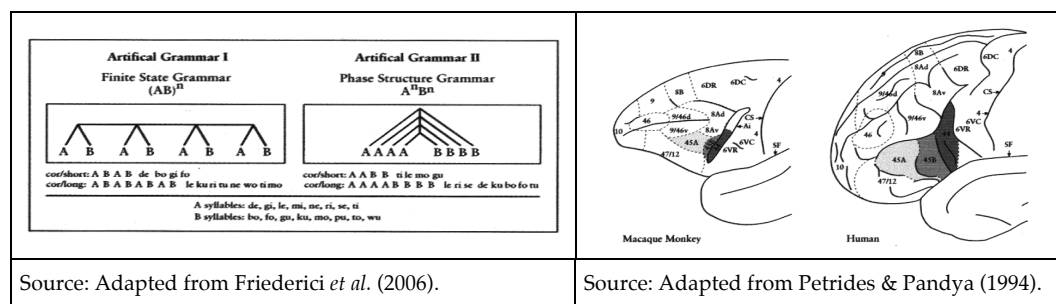


Figure 1: A difference in the kind of structures generated by Finite State Grammars vs. Phrase Structure Grammars [left]; brain imaging of the human brain and the macaque brain show differences in the size of Broca's areas (BA44, BA45) [right]

⁸ The role of Broca's areas in processing syntactic structure has been the topic of extensive research in aphasia and brain imaging studies for more than three decades (Grodzinsky & Santi 2008). Recent results from brain imaging (Friederici 2009) provide further evidence of the role of these areas (BA44, BA45) in syntactic (hierarchical) processing. See also Endress, Cahill *et al.* (2009) and Endress, Carden *et al.* (2009) on the processing of sequence peripheral positions in apes, and Mody & Fitch (submitted) on artificial grammar learning by humans, extending the standard paradigm to mildly context sensitive grammars.

⁹ See Huber *et al.* (1999) on the limits of symmetry/asymmetry visual pattern detection in pigeons, and Swaddle *et al.* (2008) on the limits of visual detection of fluctuating asymmetry in starlings.

Furthermore, work on the biological basis of vocal learning in animals, such as passerine songbirds (e.g., Jarvis 2004, 2006), has contributed to our understanding of the computational machinery behind human language acquisition. This research brings an important new perspective to our understanding of the origins and the evolution of language and its relationship to animal communication: a key shift from looking for communicative similarities or overlap to looking for common or shared competence in certain kinds of computation.

There are, however, differences between human and animal communication. The following illustrate some of these differences stemming from field studies in behavioral psychology. Studies of natural behavior have largely focused on two core properties of language: referentiality (i.e. symbol-to-world relations) and combinatorics (i.e. syntax). Field biologists have documented in vervet monkeys different specific calls in different specific contexts, while playback of those calls elicits corresponding behaviorally appropriate responses: In response to hearing the playback of an alarm call, vervet monkeys respond as if a predator was nearby. Such examples have been used to argue that animals produce vocalizations that are like our words. That is, they are formed on the basis of an arbitrary association between sound and meaning, such that each sound can trigger a representation of the target object or action—they are *functionally referential* (Seyfarth *et al.* 2005, Zuberbühler 2003). Upon closer inspection, however, the parallels between these sounds and our words are unimpressive. For example, if these animals had really evolved the capacity for referential expression of all concepts available to them, then it is unlikely that their lexicon would be limited to 10-20 ‘words’. Similarly, if their referential capacity was like ours, then animals should be able to refer to a wide range of objects and events, real or remote, past, future and imagined. But they cannot: All of the putatively referential calls they produce map onto a narrow range of actually present objects or events, even though these animals confront a wide range of social and ecological situations that are, from a functional perspective, *worthy* of comment.

With respect to combinatorial syntax, two sets of findings have entered the discussion. On the one hand, songbirds (e.g., Hailman & Ficken 1987) and whales (e.g., Suzuki *et al.* 2006) have spectacular abilities to combine their vocalization elements iteratively to create new forms in ways that could be thought of as derived by Merge. However, this combinatorial facility is independent of their conceptual system. When a songbird or whale recombines notes to produce new songs, the meaning of the signal remains the same: a sound that identifies the individual, its population or group, often to attract a mate and fend off competition. In contrast, recent studies of non-human primates suggest that when individuals combine vocalizations, these new strings are different from the meaning of each element in the string (e.g., Arnold & Zuberbühler 2006). Here too the syntactic facility is strikingly different from human language. Specifically, it operates over only two sound types and two at a time only; these types are not abstract categories such as noun and verb, or morpho-syntactic features. Thus, this primate capacity is limited to a single combination, far from the ‘infinite use of finite means’ that is the hallmark of human language.

Studies of animals trained to use human-created symbols support this

account. Animals clearly can be taught to use many symbols in a functional context, and may be able to combine these symbols. Apes can acquire several hundred symbols, sometimes apparently combined into new, meaningful strings. Yet, the rich induction that every two-year-old child makes during word learning never arises, leaving the animals with a highly fixed lexicon and children with an open-ended and explosive one. Furthermore, only human children combine words together, combining affixes and roots to form new words. Animals in these training situations are frozen at what language acquisition researchers dub the one-word stage (Terrace *et al.* 1979).

Yet, animals sometimes acquire some understanding of spoken language. Thus, one dog showed evidence of ‘fast mapping’, that is, novel word learning from minimal data (Kaminski *et al.* 2004). Studies of bonobos exposed to language suggest that individuals understand some aspects of word order and that words are classified into categories such as object, action and location (Engor *et al.* 2004). Experimental studies of language comprehension in animals are more promising than those of production, suggesting that a fundamental bottleneck in the evolution of language was the connection between linguistic computation and its externalization in linguistically meaningful structures.

4. The Genetics and Evolution of Language: Promises and Pitfalls of Modern Genomics

Until recently, very little has been learned about language from animal studies or from comparative psychology or biology. For many years, a single *idée fixe* held sway, namely, the species specificity of language—its uniqueness to humans—as well as its phenotypic uniformity within individuals. This was entirely unsatisfactory from an evolutionary standpoint, because ever since Darwin the *sine qua non* of evolutionary analysis has been both the comparative method and explicit acknowledgement of individual variation. Within the past five years, however, this picture has completely changed: Variation and concomitant evolutionary analysis is taken seriously as a biological aspect of language. It is now well-established that genes affect speech and language in individuals and there are now many demonstrable associations between inter-individual differences in genetic makeup and inter-individual differences in speech and language abilities. Perhaps the best-known is the recent *FOXP2* genomic analysis, which can be carried all the way from nucleotide variation to protein variation to embryonic development to brain function, as well as deployed for comparisons against other species including extinct hominid species like Neanderthals. But this is not an isolated example. There now exist behavioural genetic studies dissecting heritability, detailed language disorders, and language variation, all fitting into the familiar biological analysis of a complex, polygenic trait. In contrast to the classical results focusing on abnormal language and aphasias, this recent research has found that even in typical language development there appears to be genetically linked variation, some of it highly specific. Extremely detailed patterns of syntactic development, once thought to be the sole province of academic linguists, such as finiteness (tense/lack of tense) have been thrust into the biological

arena and are now known to be mostly inherited and their genetic source distinct from that of another inherited trait, phonological working memory, with established links to autism and Williams syndrome. Rounding out the connections between genetics and biology, in the case of language variation and its geographic distribution over time and space, we can now employ dynamical system analysis and computer simulations just as in population biology, accounting for the known distribution and trajectories of language variation and change, parallel to biological evolutionary ecological analysis. Taken together, such work has opened the door to how genetics might bear on the development and inheritance of particular properties of language, not just language as a whole. The following paragraphs outline some advances in our knowledge of the connections between language and genetics, as well as some of the pitfalls.

Genetics and evolutionary analysis have worked productively using the comparative approach: Looking to other species to establish parallel similarities and differences. This poses special challenges in the case of language, since no other animal species seems to fully possess the human language phenotype. What then can classical and modern genomics tell us about language's genetic and evolutionary properties? Some simple questions can be answered immediately. Classical heritability studies establish beyond a doubt that there are language components that are 'innate', that is, that have a significant genetic component, since estimates for the additive variance attributable to genes ranges between 0.4–0.6 (Stromswold 2005), roughly comparable to hair color. Likewise, as a complex behavioral phenotype, language is clearly polygenic. However, language is also labile in a special way that hair color is not, since the particular language a child speaks depends critically on the language of their caretakers, who need not be his/her genetic parents. To go beyond this broad characterization, recent research has embarked on a more precise genetic and functional dissection of language, including for the first time the isolation of at least some genomic elements that appear to have analogs in other species such as songbirds and mice. We outline just two new directions here.

One approach has opted for a more careful and systematic heritability analysis of the subcomponents of language via twin studies, revealing a closer genetic overlap between syntax and sound-structure (phonological) abilities and fine motor control than syntax and the lexicon (Stromswold, *in press*). Going forward, by pushing conventional quantitative trait loci (QTL) methods to their limits, we may be able to characterize even more finely the differences between conventional linguistic categories such as syntax, phonology, the lexicon, and semantics (Stromswold, *in press*; see also Stromswold 2001, 2006, 2008). More speculatively, given the availability of high-throughput whole-organism genome scans, we may be able to supersede conventional QTL, as has been done in other polygenic cases like Alzheimer's syndrome, since it has now become feasible to test all of an organism's genes directly for association with some trait of interest. In the present case, what this means is that for some very particular syntactic ability, we may be able to identify a candidate gene set correlated to this trait.

Current research has embarked on a more precise genetic and functional dissection of language. This was recently sparked by the discovery of a Mendelian point mutation linked to a rare language disorder across several gen-

erations in a single British family. While the exact phenotypic manifestation of this disorder remains open to debate, many agree that the disruption results in so-called 'verbal dyspraxia', including a general inability to orchestrate coordinated mouth movements. However, a range of language and non language abilities are apparently impacted, including written language as well as phonological working memory (Fisher *et al.* 2003, Watkins *et al.* 2002). Researchers eventually identified, cloned and sequenced the gene in question, *FOXP2*, making it the first discovered gene causally linked to language (Hurst *et al.* 1990, Vargha-Khadem *et al.* 1995, Fisher *et al.* 1998, Lai *et al.* 2000, Lai *et al.* 2001, Vargha-Khadem *et al.* 2005). It is one of a subclass of an evolutionarily well-known family of 'forkhead box' transcription factor genes whose protein product interacts with DNA, thus regulating other genes.

The discovery of the *FOXP2* gene was initially greeted with great enthusiasm. It was the first specific genetic window into human language development and evolution, and offered hope of linking human and animal studies into one, with the possibility of testing an animal model. However, subsequent analysis strongly suggested that the protein transcripts of this gene, *FOXP2*, might not be implicated directly in the central computational aspects of language. Individuals with the language deficit have sequential control motor deficits not limited to language syntax (Haesler *et al.* 2004, Hauser & Bever 2008). Its role in other species suggests that it underlies a general vertebrate sensorimotor system for fine motor control and 'higher level' sequential movement planning. For example, *FOXP2*'s homologues have been implicated in the production, learning and perception of songs in oscine songbirds (Webb & Zhang 2005, White *et al.* 2006, Teramitsu & White 2006, Haesler *et al.* 2004) with *FoxP2* expression boosted during the seasonally plastic song-learning periods. Further, *FoxP2* suppression in the zebra finch song-learning brain area leads to inaccurate song imitation and acquisition by juvenile learners (Haesler *et al.* 2007). *FoxP2* has also evidently been undergoing recent rapid evolution perhaps linked to the vocal-learning of certain bats (Li *et al.* 2007). It may even be related to the proper development of ultrasonic calls in mouse neonates (Shu *et al.* 2005, Fujita *et al.* 2008, Groszer *et al.* 2008). Thus, *FOXP2*'s role in human language may underlie part of the machinery that builds the sensorimotor system for fluent speech. Neural activity studies in the affected family (Vernes *et al.* 2006) had promoted the view that *FOXP2* affects the regions involved in general planning of fine motor output, sensorimotor integration, and multimodal sensory processing, as opposed to circuitry controlling mouth and lower face movements. Genetically engineered mice exhibit altered motor control learning (French *et al.* 2007, Groszer *et al.* 2008), which seems to support the initial consensus that *FOXP2* is critical for learned motor skills rather than language *per se*. However, Teramitsu & White (2006) showed that the expression of the gene is different depending on whether the bird's song is directed or undirected. The motor control is the same, but the expression of the *FoxP2* gene is different (there is down-regulation in the undirected singing vs. slight up-regulation in the directed singing).

The *FOXP2* discovery also jump-started modern evolutionary Biolinguistics. There are just two functional amino acid differences between *FOXP2* and its variant in chimpanzees, plus one additional difference with the variant in

mice. The two human–nonhuman primate differences have been interpreted as the effect of accelerated evolutionary change in the 4.6–6.2 million years that separate us from the chimpanzee, possibly with a faster rate within the last 50–100,000 years, and have been posited as the target of positive natural selection, perhaps concomitant with language emergence (Enard *et al.* 2002). Not surprisingly, the causal relationships between these two changes and language remain unclear. Further, cautionary notes must be sounded regarding the contributions of selective processes as opposed to non-selective processes such as biased gene conversion (Berglund *et al.* 2009, Duret 2009, Hodgkinson *et al.* 2009).

Our understanding of *FOXP2* has itself evolved, unsurprisingly since *FOXP2* is one of the largest and most complex regulatory genes known. The initially clear-cut, one-gene–one-behavioral phenotype FoxP2 picture has been replaced with a much more nuanced ‘molecular network’ systems view (Fisher & Scharff 2009) in which many ‘downstream’ cognitive systems might be affected by the *FOXP2* gene. Taking into consideration the words/non-word repetition task deficits that the KE family members exhibit (Watkins *et al.* 2002), some have suggested a relation between the regulation of the expression of *FOXP2* and procedural or working memory (Bosman *et al.* 2004, Ullman & Pierpont 2005). Building on this general approach, although focusing on the specific memory specifications that phrasal manipulation requires (basically, a push-down automaton), Piattelli-Palmarini & Uriagereka (2005) propose that such matters are relevant to architectural computational concerns in competence systems. On the basis of reduced activity in Broca’s area, still others suggest a possible link with mirror neurons (Corballis 2004). Furthermore, the interesting parallel with the expression of the gene in songbirds has suggested a possible role for *FOXP2* in the linearization of complex hierarchical structures into a linear sequence, as well as its reconfiguration, upon successful processing into the original internal structure (Piattelli-Palmarini & Uriagereka, *in press*).

Moreover, Vernes *et al.* (2008) found that *FOXP2* binds to and dramatically down-regulates *CNTNAP2*, a gene that encodes a neurexin and is expressed in the developing human cortex. On analyzing *CNTNAP2* polymorphisms in children with typical specific language impairment, they detected significant quantitative associations with nonsense-word repetition, a heritable behavioral marker of this disorder. Intriguingly, this region coincides with one associated with language delays in children with autism (Piattelli-Palmarini & Uriagereka 2005, *in press*). Currently there is no way to decide among these various possibilities, since we are still uncovering important new details about the basic genetics of this complicated system. (For example, recently it has been found that *FOXP2* is itself regulated by a host of so-called ‘small RNAi’ or sRNAi molecules (Friedman *et al.* 2009) and a new *FOXP2* transcription ‘start site’ was also discovered (Schroeder & Myers 2008).) So, we have some distance to go in understanding the complete FoxP2 picture. Nevertheless, all this is an advance, not a retreat, since *FOXP2* will undoubtedly serve as a role model for future genomics research about language. While it remains an unfinished task to identify the final causal links to language impairments, the discovery and analysis of this gene and the genes that it regulates have served as an extremely useful example of how to unravel via genomics the complex phenotype that is human language.

5. Language Development and Genetics: The Case of Tense

Within the last decade, there have also been major advances in our understanding of language development, especially the precision, replicability, and meaningfulness of particular results. For the first time we are in a position to state surprising and non-trivial results about the nature of language development. The traditional idea was a false-to-fact idealization about instantaneous development, as if information was available to the child at a single point in time. Current practice and results turn this original notion on its head, rendering the concept of child's biological development central rather than peripheral. In this sense, the classic work on language and biology—Lenneberg's (1967) *Biological Foundations of Language*—was right, but appeared still-born. We wish to point out some new results and sketch how they fit into a broader biology. New methods make this possible: The level of quantitative precision about computationally precise developmental linguistic behaviors has raised the descriptive bar by an order of magnitude compared to a decade ago. In some cases, the results bear a striking resemblance to scientific laws. Further, it is a truism that human language capacity combines learned and genetically-transmitted abilities, and we must therefore take seriously the interaction of genetics and language. For the most part, this is currently accomplished via studies of deviant populations. In the past this had proved difficult because we lacked the requisite information about typical development. Given major advances in the field, we can now study impaired populations, and a surprising number of regular results are beginning to be uncovered across a range of linguistic and cognitive deficiencies. These findings seem to hold great promise in the quest for genetic understanding; for instance, for the first time, both behavioral genetic and linkage studies are being carried out in the normally developing child as well as in children with selective impairments. We will review these—what is already known and what can be accomplished in the (near?) future. These new methods involve an exquisitely precise understanding as to how linguistic representations develop, and how to relate these to concrete deficiencies.

Language development may be influenced by general learning procedures, Bayesian inference serving as a prime instance currently under investigation in many research programs. In that light, a central question for Biolinguistics is which, if any, specialized structures have evolved in the service of such processes for language in particular, which have developed for cognition in general, and which are only accidentally affected by such inferential mechanisms in individuals. In the last 20 years, there has been intense study of the early computational system of language in children. The results show that very young children 'learn' basic properties unique to their language much faster than unguided learning models could predict. Such phenomena have motivated linguists to postulate a strong genetic component that pre-figures possible languages in the child's mind, as is typical of species-specific 'learning' in general. Furthermore, the ability to acquire language as a first language decays rapidly after puberty (Lenneberg 1967). Research investigating the cognitive and neural bases of language acquisition addresses the following questions about this phenomenon: How abrupt is this diminution in language learning ability? Is it an averaging effect? Are all

aspects of language affected equally and at the same time?

In the following sections, we discuss molecular genetic studies of second language learning, as well as behavioral genetic studies (twin studies, family aggregation) of second language learning, shedding light on a deeper understanding of why there is a critical period for language acquisition. Current research explores the impact of sex hormone levels on language learning using the variability in onset and duration of puberty in a variety of clinical and normal populations. The investigation of the relationship between genetics and the so-called critical period, for example, molecular genetic studies of second language learning, as well as genetic studies of second language learning, permits a far deeper understanding of why there is a critical period, how it is related to learnability theory, language processing, and language evolution, as well as unraveling the relationship between language learning and neural activity and its structure.

5.1. *Very Early Clause Structure Variation*

Although basic properties of language may be genetically determined, languages differ in some experience-determined ways. For example, unlike English, Dutch and German are examples of languages that are called ‘verb-second’ (V2): The verb in the main clause always comes second in the sentence (otherwise it is always at the end of the clause) and is tensed (e.g., present or past), regardless of what comes first. Any other part of the clause may be in the 1st position. The German sentence *Das Buch hat Johann* ‘the book has John’ (meaning ‘John has the book’) shows the verb *hat* ‘has’ in 2nd position, though *das Buch* is not the subject. Only verbs that show ‘tense’ can enter the V2 (Tense) position. In adult language, all main clauses have a tensed verb. Yet, young children very often omit tense, producing an ‘infinitival’ verb (an ‘Optional Infinitive’) like *Johann das Buch haben* ‘John the book (to) have’ (Wexler 1993, Poeppel & Wexler 1993, Haegeman 1994, Guasti 2002). Why is this? If children know that their language is V2, they should place tensed verbs in 2nd position and only verbs without tense in final position. Many studies of the sentences spontaneously pronounced by young children speaking V2 languages show that this prediction is borne out almost perfectly (Poeppel & Wexler 1993, Haegeman 1994, Wexler *et al.* 2004). For example, Wexler *et al.* (2004), studying 2,590 utterances of Dutch children between 1;7 and 3;6 years of age, found that about 1% of the utterances violated the prediction. This developmental pattern holds in all V2 languages studied so far. Children learn the V2 pattern very early and well, suggesting that children are brilliantly plastic with respect to certain variable features that differentiate languages. They do not, however, retain this plasticity.

5.2. *Why Untensed Verbs?*

Why do young children use so many verbs without tense in simple clauses, which are violations in the adult language? The systematic nature of their patterns shows that this is not a trial-and-error phenomenon. One hypothesis (Wexler 1998, 2003) is that children are subject to a computational constraint that does not allow both Tense and Agreement features to be simultaneously

operative. Therefore they omit either tense or agreement, producing an optional sentence-final infinitive. This proposal goes beyond the case of German and Dutch: For example, it predicts that young children in English often produce forms like *him go*, using an 'object' pronoun in subject position, but only with an untensed verb. This constraint also explains other phenomena of early language development in various languages (Wexler 1998, 2003), including many phenomena that appear on the surface to be unrelated, such as the omission of object 'clitics' (i.e. weak forms of object pronouns occurring in preverbal position) in French and Italian (Jakubowicz *et al.* 1997, Jakubowicz *et al.* 1998, Hamann 2002, Paradis *et al.* 2005/2006).

5.3. *Development*

One developmental hypothesis is that the computational constraint 'grows away' as a result of maturation, under genetic guidance. More traditional psychological hypotheses about learning do not seem to be adequate explanations. For example, input to the child overwhelmingly has tensed verbs in simple clauses, so children are not imitating what they mostly hear. The child's tenseless forms are not 'simpler'—they are often more superficially complex than the correct tensed forms, for example, the correct *werk* 'work' is replaced by *werken*. Standard environmental variables that are known to increase learning (Huttenlocher *et al.* 1991) have no such effect on the development of tense (Rice *et al.* 1998).

Behavioral genetic studies provide evidence for the heritability of the use of tensed constructions. A study of typically developing twins showed that the development of tense is closer in identical twins than in fraternal twins (Ganger *et al.* 1997). Further support for the biological basis for tense comes from studies of Specific Language Impairment (SLI), a condition in which children have difficulties in language, often with no apparent general cognitive deficit: They show frequent tense omission (Rice *et al.* 1995, Rice & Wexler 1996, Wexler 1996, 2003, Rice *et al.* 1998, Wexler *et al.* 2004). SLI is a genetically caused difficulty, on our interpretation involving a persistence of the early computational constraints. In fact the use of optional infinitives extends at least through the teen years, suggesting that the tense deficit may be permanent (Rice *et al.* 2009). A large study of 6-year-old twins at risk for language delay (Bishop *et al.* 2005) measured subjects' ability to repeat nonsense words, a test of the use of tense, and several other behaviors, including vocabulary size. Figure 2 shows their results.

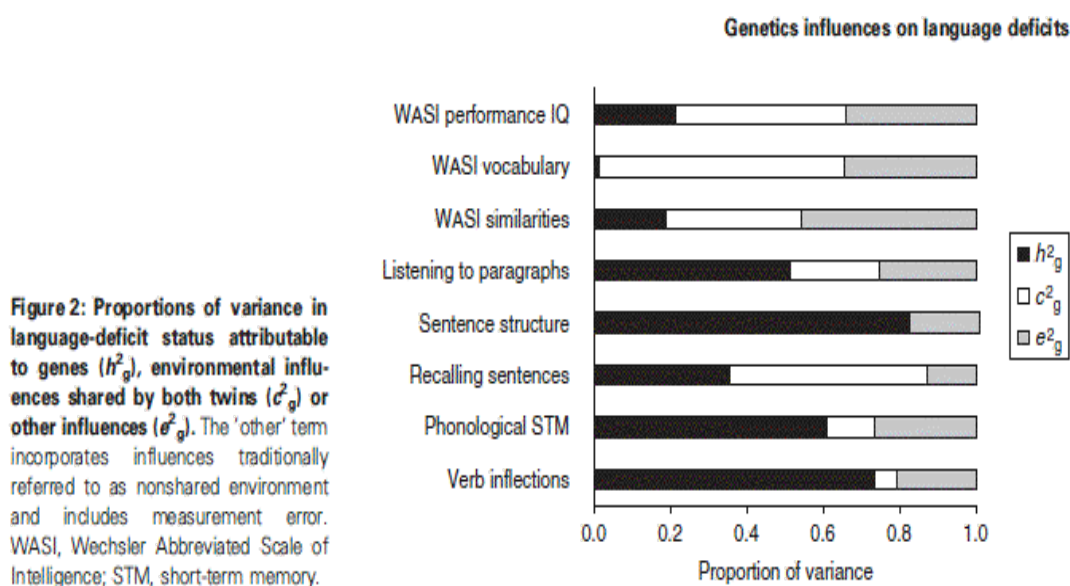


Figure 2: Proportion of variance in language-deficit status

The vocabulary measure WASI (Wechsler Abbreviated Scale of Intelligence) has almost no heritable component. Both phonological short-term memory (STM) (the ability of people to hold uninterpreted phonological strings in mind, usually measured by how well they repeat nonsense words) and frequency of the use of tense ('inflections') have very strong heritable components. But the bivariate heritability of phonological STM and tense was close to zero. Thus, the authors argue, the development of tense is independent from pure phonological memory.

There are probably two distinct forms of SLI, one related more to memory impairment, and one related more to linguistic impairment (including tense use). Several studies (The SLI Consortium 2002, 2004) have linked phonological memory to a region (*SLI1*) of chromosome 16 while Falcaro *et al.* (2008) have linked tense development to a region *SLI2* of chromosome 19. We can cautiously infer from this result that there is a chromosomal region somehow related to the optional infinitive genotype, perhaps to the growing away of the computational constraint. These methods and these kinds of data show that it is possible to find (regional) linkage for a particular aspect of language processes. Hypotheses developed in linguistic theory led to studies of the development of tense deficit in children and the discovery of the optional infinitive stage that led to the discovery of the extended nature of that stage in SLI children which led to linkage of variation in these properties to regions of the genome. Each of these steps involved creative research, but they exemplify what we hope for the future.

6. Normal Variation in the Neurology of Language and the Genome

The study of *FOXP2* and SLI exemplifies the common method of exploring genes' potential functions by noting the disastrous impact their mutations can have on

normal behavior or structure. In the case of studying the genetics of language in humans, we want to focus on just those cases that, according to numerous publications on these pathologies, spare general cognition and reduce language (SLI, in general) or conversely reduce general cognition and spare language (e.g., Williams syndrome; see Bellugi *et al.* 1994, Bellugi *et al.* 2001, Clahsen & Temple 2003, Zukowski 2005). But a gap in one kind of human ability allows behavioral and cognitive compensatory mechanisms to come into play, thus obscuring or at least confounding the data. Consequently, it is useful to also consider cases of 'normal' variation in language representation related to genetic variation, whenever possible. This possibility has recently arisen. It involves the neurological organization for language as a function of left- vs. right-handed family background.

Language scientists have long struggled with the problem of how our internal dictionary (the lexicon) is processed in relation to syntactic composition: Is the lexicon distinct from syntactic computation? How are words integrated with syntax? Recent explorations of potential genetic differences in how words are stored shows how biology and language can fruitfully interact and further dissect the general grammatical scheme in (1) all the way to genomics. This comes from current research on language acquisition and on the brain's division of the cerebral cortex into left and right halves. A familiar biological-language asymmetry is that almost all right-handed people possess strong left hemisphere lateralization for syntactic function. However, research on certain kinds of aphasia—the pathological traumatic inability to produce or comprehend language—has revealed that right-handers with left-handed family members ('mixed families') display more right hemisphere language involvement than right-handers whose other family members are only right-handed ('pure families'; see Luria 1970, Hutton *et al.* 1977). More recent behavioral research has shown that individuals from mixed families access individual words more readily than sentence structure, while the reverse is true for pure family right-handers: Accordingly, the right hemisphere's language involvement may be specific to the lexicon (Bever 1983, Bever *et al.* 1987, Bever *et al.* 1989, Townsend *et al.* 2001). Furthermore, the critical language learning period for mixed family right-handers comes earlier than for individuals from purely right-handed families (Ross & Bever 2004), possibly because mixed family right-handers base their language acquisition learning on words as opposed to syntax. This conjecture has found recent support in an fMRI study showing greater right hemisphere activation for a lexical task in right-handers with familial left-handedness (see discussion in Bever 2009).

These findings on laterality confirm the basic hypothesis that mixed family right-handers have more distributed lexical knowledge. The next step will be to unravel the behavior and brain activation patterns of mixed family right-handers with and without the gene markers recently associated with left-handedness (Francks *et al.* 2007). The literature focusing on syndromes such as schizophrenia and Alzheimer's provides some models of studying normal cognitive variation in relation to genetic variation (Egan *et al.* 2003, DeYoung *et al.* 2008, Green *et al.* 2008, Tan *et al.* 2008). The case of familial handedness will be complete if only those with left-handedness genes exhibit lexically focused behavior, opening a

new window into language's genetic base and its variation in an ostensibly normal population. In addition, further research remains to demonstrate that specifically syntactic information about words is bilaterally accessed, not just word associations: For example, while *sneeze* is syntactically an intransitive verb, 'sneeze' also has strong semantic associations with 'flu' and 'sick'. Words might still be represented bilaterally in people with familial left-handedness, with syntactic information represented in the left hemisphere and associative information in the right. However it plays out, such case studies will expand our scientific understanding of the interplay between the genome, the brain, language behavior, and grammar, sharpening our understanding of the genetic endowment for language.

7. Conclusion

Advances in theoretical linguistics, comparative ethology, genetics, and language evolution contribute to our knowledge of the biological basis of language and pave the way to what is yet to be explored in Biolinguistics. No doubt, many of the recent discoveries and theories will be modified by ongoing research, logical considerations, and new methodologies. The main point of this review is to show how the study of language can be integrated around scientific questions familiar to biologists and ethologists. We started with a formal analysis of what language *is*. These features were then discussed in light of studies of animal behavior, both natural and experimentally induced. Next, we turned to more direct genetic investigations of language dysfunctions, first in a familial phenotype, then a developmental one. Finally, we considered potential genetic influences on the neurological organization of language. Thus, we have outlined a range of typical biological methods as applied to the integrated study of language as a biological phenomenon with a critical genetic component. The results are still fragmented and subject to revision. But we are confident that a coherent picture of language as a biologically rooted phenomenon will emerge out of investigations of these kinds.

The Biolinguistic Program links language and biology in a natural way. Moreover, it proposes architectural properties of FLN and properties of the discrete infinity of human language that serve as a useful guide for further investigation of other human systems, of non-human species and their neurological organization. Additional questions arise however: How can the recursive hierarchical structures derived by Merge be further tested in humans? And what evidence can be brought about for its presence/absence in animals? While a few preliminary results are available, further neurobiological experiments are necessary. Moreover, we have pointed out some promises and pitfalls of modern genomics, and further work is needed to understand the pathways from genes to linguistic phenomena. Addressing these questions and formulating hypotheses that are testable on different populations will pave the way to a further understanding of the biology of human language.

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Anna Maria Di Sciullo
 Université du Québec à Montréal
 Department of Linguistics
 P.O. Box 8888, Downtown Station
 Montréal, QC H3C 3P8
 Canada
Di_Sciullo.Anne-Marie@uqam.ca

Kenneth Wexler
 Massachusetts Institute of Technology
 Department of Brain and Cognitive Sci-
 ences & Department of Linguistics
 and Philosophy
 77 Massachusetts Avenue, 46-2005
 Cambridge, MA 02139
 USA
wexler@mit.edu

Cedric Boeckx
 ICREA & Universitat Autònoma de Barcelona
 Departament de Filologia Catalana
 7Edifici B, Campus UAB
 08193 Bellaterra (Barcelona)
 Spain
Cedric.Boeckx@uab.cat

Juan Uriagereka
 University of Maryland at College Park
 Department of Linguistics
 1102 Marie Mount Hall
 College Park, MD 20742
 USA
juan@umd.edu

Lisa Lai-Shen Cheng
 Leiden Universiteit
 Department of General Linguistics
 2300 RA Leiden
 The Netherlands
L.L.Cheng@let.leidenuniv.nl

Andrew Wedel
 University of Arizona
 Department of Linguistics &
 Program in Neuroscience
 Tucson, Arizona 85287
 USA
wedel@u.arizona.edu

Elly van Gelderen
 Arizona State University
 Department of English
 Tempe, Arizona 85287
 USA
EllyVanGelderen@asu.edu

Massimo Piattelli-Palmarini
 University of Arizona
 Department of Linguistics, Program in Cognitive
 Science & Department of Psychology
 Tucson, AZ 85721
 USA
massimo@email.arizona.edu

Robert C. Berwick
 Massachusetts Institute of Technology
 Department of Electrical Engineering and
 Computer Science & Department of
 Brain and Cognitive Sciences
 77 Massachusetts Avenue, 46-2005
 Cambridge, MA 02139
 USA
berwick@csail.mit.edu

Lyle Jenkins
 Biolinguistics Institute
 Cambridge, MA 02139
 USA
LJenkins2@comcast.net

Karin Stromswold
 Rutgers University at New Brunswick
 Department of Psychology &
 Center for Cognitive Science
 152 Frelinghuysen Road
 Piscataway, NJ 08854
 USA
karin@rucss.rutgers.edu

Heidi Harley
 University of Arizona
 Department of Linguistics &
 Program in Cognitive Science
 Tucson, Arizona 85721
 USA
HHarley@email.arizona.edu

James McGilvray
 McGill University
 Department of Philosophy
 Montréal, QC H3A 2T5
 Canada
James.McGilvray@mcgill.ca

Thomas G. Bever
 University of Arizona
 Department of Linguistics &
 Department of Psychology
 Tucson, Arizona, 85721
 USA
tgb@email.arizona.edu