Prolegomena to a Future Science of Biolinguistics

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This essay reviews some of the problems that face biolinguistics if it is to someday succeed in understanding human language from a biological and evolutionary viewpoint. Although numerous sociological problems impede progress at present, these are ultimately soluble. The greater challenges include delineating the computational mechanisms that underlie different aspects of language competence, as implemented in the brain, and understanding the epigenetic processes by which they arise. The ultimate challenge will be to develop a theory of meaning incorporating non-linguistic conceptual representations, as they exist in the mind of a dog or chimpanzee, which requires extensions of information theory incorporating context-dependence and relevance. Each of these problems is daunting alone; together they make understanding the biology of language one of the most challenging sets of problems in modern science.

Keywords: biolinguistics; comparative method; computation; deep homology; neurobiology of language

1. Introduction

> ***Prolegomena*** *(from Greek, plural noun, singular prolegomenon) — a preliminary discourse, statement or essay prefixed to a book, etc.*

In the first years of the new millennium, the word 'biolinguistics' has rather suddenly come into use as an umbrella term for various biological approaches to the study of human language. At least three recent books have 'biolinguistics' in the title (Givón 2002, Jenkins 2000, 2004), the journal *Biolinguistics* was founded (www.biolinguistics.eu), and the first Laboratory of Biolinguistics (Riken Brain Science Institute, Japan) is producing its first generation of PhD students. Based simply on the divergent contents of the books mentioned above, this nascent field is broad in its interests and incorporates diverse viewpoints, both about what language is and how it should be studied. Despite numerous disagreements, what the scholars embracing this term all have in common is the core belief that

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the human capacity to acquire and use language is an aspect of human biology, and that it can thus be profitably studied from a biological perspective. While this core assumption of biolinguistics is not particularly new (Chomsky 1965, Darwin 1871, Lenneberg 1967, Lieberman 1975), it appears to be an idea whose time has come. Biolinguistics is not yet a science — it is more a loosely-defined collection of questions and approaches — but it certainly has the *potential* to become a science. The purpose of the current article is to survey this potential, and to highlight some problems that stand in the way.

2. The Promise of Biolinguistics and Obstacles to Progress

It is certainly an opportune time for scientists interested in human cognition to adopt a biological perspective, since the suite of tools available to support empirical inquiry into all aspects of biology have recently become so powerful. Human brain imaging techniques are now widely available, unthinkable a few decades ago, that allow us to examine neural function noninvasively, in normal subjects. After a decade or so of somewhat self-indulgent neo-phrenology, this field shows signs of maturing into a promising endeavor with important advantages over the patient-based approaches to neurolinguistics that preceded it. These tools will help map the functional circuits underlying language competence, and ultimately help point the way to the underlying neural computations that are of central interest. Behavioral techniques for investigating language and related cognitive functions, including eye tracking and looking time techniques, are unveiling a complex cognitive world in pre-verbal infants and non-verbal animals that stands in sharp contrast to their limited communicative ability. Finally, and perhaps most profoundly, the revolution in molecular genetics has produced genome sequences of humans, chimpanzees, dogs and many other species, and gene sequences of humans turn out to be nearly identical in many cases with homologous genes in chimps, mice, flies and even yeast. Genes involved in diverse aspects of human cognition are being pinpointed, and we can now both observe and control gene expression in animal models.

These and other new techniques are generating a flood of empirical data relevant to age-old questions about the development and evolution of language and the mind. These data often demand fundamental changes in entrenched ways of thinking about these problems. For instance, accumulating results and animal and infant cognition belie the belief that language is a pre-requisite for any form of complex conceptual processing. Similarly, the new results from developmental molecular genetics necessitate profound changes in traditional conceptions of ‘innateness’. Thus, more than ever before, the biological approach to language has much to offer the linguist, psychologist, anthropologist, and philosopher. Problems that once seemed insuperable, such as interactions between ontogeny, cultural ‘evolution’, and phylogeny, are slowly yielding to concerted theoretical and empirical effort (Deacon 1997, Kirby, Dowman & Griffiths 2007, Kirby, Smith & Brighton 2004, Steels 1999, Tomasello 2001).

But there is trouble in this potential interdisciplinary paradise, and despite considerable grounds for optimism, it is by no means certain that the new biolinguistic approach will be as successful and productive as it deserves to be. As I see it, the problems facing a future science of biolinguistics come in two flavors. The first, and the less challenging intellectually, are essentially sociological problems concerning terminology, disciplinary turf wars, and struggles for dominance. A reliance on oversimplified models and outmoded distinctions is another important sociological impediment to progress. Although these problems are easily diagnosed, they may be difficult to solve. Fortunately, some of the more deeply-entrenched and recalcitrant disciplinary divides and outmoded debates and dichotomies seem to be breaking down, and I am optimistic that the next generation of young biolinguists, for whom disciplinary boundaries are more fluid, will eventually leave many of these sociological problems behind.

The second class of problems involve far more profound theoretical difficulties, and constitute some of the most serious intellectual challenges of our time, or indeed that science has ever faced. It is on these difficulties that I focus in this essay. I see three broad areas of conceptual challenge, each of them related to the others, and all three demanding fundamental theoretical and empirical progress before we can hope to understand the biological basis for language. The first challenge is *neuroscientific*: Despite huge progress, at a basic level we still do not understand how brains generate minds. This is as true of a dog's brain as for a human's, and it is true of very basic aspects of cognition, such as vision and motor control, along with language. The most fundamental neurolinguistic questions concern the basic computations underlying language use, and their specific neural basis. Current attempts to address this question remain on a shaky theoretical footing. The second challenge concerns genes and *development*: How do genes control the development of a single-celled zygote into the trillions of integrated cells comprising a complex behaving organism? Again, great progress has been made, and the new epigenetic paradigm allows us to reject long-reigning models of the genome as blueprint. However, the complex and circular nature of epigenesis, and the resultant causal indirectness of development, still pose serious conceptual challenges. While we now understand in some detail how physical structures like the vertebrate limb develop, the principles underlying brain development and evolution remain only dimly understood.

Finally, while the neuro-computational and developmental difficulties are basically biological, and apply to *any* aspect of cognition, the last and I fear most profound difficulty concerns language more specifically. This suite of problems concerns questions of *meaning*. Put simply, we have a good theory of information (Shannon information theory), but we lack anything even approaching a good theory of meaning (what I intend with this information/meaning distinction will become clear below). Problems of reference, relevance and context-dependent interpretation remain central unresolved issues in the philosophy of mind. While the first two problems have matured to a stage where they appear to be accepted as problems of the empirical natural sciences, these last problems remain in the philosophical category. (We don't even know how to devise experiments to help sort the issues out.) While these unsolved semiotic challenges pose problems for any aspect of cognition (what is it that happens when an organism interprets some stimulus as 'meaningful'), they become particularly acute when discussing language, which is that aspect of cognition centrally concerned with meaning.

Recent reviews of new approaches and data in biolinguistics are already available (Fitch 2005b, in press, and Johansson 2005). Therefore, my goal here will rather be to outline and clarify the problems facing the field. As one interested in seeing this field flower and grow, I intend my critical comments to be constructive. I have been working in 'biolinguistics' (without knowing it) for the last 15 years, since my decision as a young marine biologist to refocus my efforts on the evolution of language (e.g., Fitch 1994). Although I remain optimistic, I have become acutely aware of the difficulties facing the field, in part because successes in various areas have brought the remaining problems into sharper focus. Through my involvement in a recent interdisciplinary foray in biolinguistics (Hauser *et al*. 2002) and the debate that followed (Pinker & Jackendoff 2005, Fitch *et al*. 2005), I have also developed a healthy (if depressing) awareness of the sociological problems that await attempts at interdisciplinary bridge-building.

In this article I will start by briefly discussing the sociological problems and disciplinary strife that arise from choices in terminology and differing conceptions of 'language'. These pose important but soluble problems for those with a *bona fide* interest in solutions, I think, and will not be my core focus here. In the main part of the article I will outline and clarify some of the deeper intellectual challenges facing biolinguistics, discussing why many currently-popular models and metaphors for understanding genes, brain and language need to be abandoned if we hope to make substantial progress. In some cases I will also try, tentatively, to sketch approaches to the problem that appear to me to offer promise. But I will be satisfied if the reader, accepting my critique of the 'state of the art', rejects my proposals for remediation. Each problem alone is extremely difficult, and combined as they must be in biolinguistics, even guessing at plausible answers is difficult. In this essay, as with any prolegomenon, my focus is making the problems sharp and clear, rather than defending particular solutions.

2.1. *Sociological Challenges: Disciplinary Discord and Terminological Debate*

> *The chance that the key ideas of any professional scholar's work are pure nonsense is small; much greater the chance that a devastating refutation is based on a superficial reading or even a distorted one, subconsciously twisted by a desire to refute.*
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> (Langer 1962: ix)

This wise insight accurately diagnoses much contemporary 'debate' in biolinguistics, particularly concerning the evolution of language. I know of no other field where scholars seem so ready to champion their own pet hypothesis uncritically, while rejecting those of others as ludicrous. While I confess to finding some proposals in the literature uncompelling on first reading (e.g., the 'Throwing Madonna Hypothesis' (Calvin 1983), or the 'Aquatic Ape Hypothesis' (Morgan 1997)), further reading and thought have convinced me that some valuable insights, and probably germs of truth, are to be found in such ideas — for one willing to put in the work of understanding them. Unfortunately, such willingness is too often in short supply, and debate in the biology and evolution of language frequently reduces to either misrepresentation (dismissals based on straw-man caricatures) or arid terminological debates ("I dislike the term *X* for some trait and propose term *Y* for the same thing"). Often the two are combined.

This syndrome is particularly true of criticisms of Noam Chomsky, whose ideas so many scholars apparently love to hate. In my opinion, once placed in context and properly understood, most of Chomsky's scattered statements about both language evolution and its biological bases either are rather uncontroversial statements that any modern biologist studying, say, limb development would accept as a matter of course (e.g., that there must be various biological constraints upon the development of the language system), or statements of unpopular alternative hypotheses that deserve more careful consideration (e.g., language as a tool for thought rather than communication). Outside of his technical linguistics work, Chomsky's main contribution to biolinguistics is his long championing a scientific approach to language as a *biological* phenomenon (Chomsky 2005). One will search in vain in Chomsky's own writings for the naive conceptions of Universal Grammar for which he is so often mistakenly pilloried — one reason his critics typically quote his few scattered statements out of context, if they quote them at all.

My purpose in this article is neither to champion nor to attack Chomsky's conception of language (for this, see, e.g., Jenkins 2000, Lieberman 2000, Jackendoff 2002, Boeckx 2010) — but rather to argue that such discussions too often miss or leave unmentioned deeper commonalities of viewpoint and approach shared by most contemporary theorists interested in the biology of language. In the next sections, I will try to look past the terminology at some uncontroversial facts about the biology of language, briefly discussing the terminological controversies they have driven. My purpose is to shed the rhetoric and move into the conceptual heart of biolinguistics. This will set the stage for the main part of the article, where I discuss the core outstanding conceptual difficulties in detail.

2.2. *'The Human Capacity to Acquire Language': The Core Explanandum*

The central research topic in biolinguistics is a characterization and explanation of the human capacity to acquire and use language. That this is an aspect of human *biology* is made clear by the everyday fact that any normal child raised in a human household will quickly, and apparently effortlessly, acquire the language(s) of its family and community, while no non-human animal will do the same. The pet dog or cat may learn quite a bit about the social and practical aspects of life in a human household, and often to recognize a few dozen spoken words of the local language, but its abilities to *express* its own thoughts *using* this language are little different from those of a potted plant in the living room. Perhaps more surprisingly, a chimpanzee raised in a human home will not spontaneously do much better: Even with long and intensive training, young apes learn to produce only an indistinct handful of inarticulate words (Yerkes & Yerkes 1929, C. Hayes 1951). Although use of the manual/visual modality via sign or symbols helps young apes considerably (Gardner & Gardner 1969, Premack 1971), the adult ape still cannot progress to anything like the level of a five-year old child, and its 'linguistic' utterances will be mostly confined to requests for tickles or treats. While not belittling the accomplishments or value of such experiments (cf. Savage–Rumbaugh 1986, Savage–Rumbaugh *et al.* 1993), it is important to acknowledge these limitations as well-replicated biological facts.

Clearly, immersion in a linguistic *environment* is not enough for spoken language to develop in most organisms. There must therefore be *something* about human children which differentiates them from other species, and this something provides one of our core *explananda* in biolinguistics. We might gloss this neutrally as 'the human capacity to acquire language'. In generative linguistics this capacity is traditionally called the 'Language Acquisition Device', and a characterization of its properties termed 'Universal Grammar' (Chomsky 1965, reviving a 17th century term). Universal Grammar (before Chomsky) simply designated those aspects of human language competence which, because they are shared by all humans and all languages, went unmentioned in traditional grammars (Chomsky 1966, Allan 2007). For example, the notion that words exist and have specific meanings does not need to be specified in a grammar of French — it can be taken for granted. But this is precisely the sort of fact that *does* need to be explained by a successful biological approach to language. The original usage of the term made no particular claims about the nature of this competence (e.g., that it was specific to language, or conversely a general aspect of human cognition), nor did Chomsky's revival of the term, which is quite neutral on such questions by my reading. However, both 'Language Acquisition Device' and, especially, 'Universal Grammar' arouse suspicion and rejection from scholars who nonetheless accept that such a human-specific biological capacity exists (e.g., Lieberman 1998a, Tomasello 1999, 2005). A huge amount of ink has been shed rejecting the term 'Universal Grammar', even by people who accept without question that a biologically-based capacity to acquire complex language fully is a uniquely-powerful birth-right of any normal human, but no known animal. The substantive debate concerns not the *existence* of such a human capacity for language acquisition, which is abundantly clear regardless of terminology, but rather its nature (e.g., the degree to which it is specific to language).

There remains, today, no widely-accepted term for this central aspect of human biology, despite the consensus about its existence. A recent attempt to break the resulting terminological logjam by introducing two new terms — the faculty of language in broad and narrow senses (FLB and FLN; Hauser *et al.* 2002) — unfortunately elicited similar reactions (e.g., by Pinker & Jackendoff 2005), although FLB was specifically and explicitly intended to capture a much broader and more inclusive conception of the language capacity than the one connoted by Language Acquisition Device or Universal Grammar. FLN was intended to have a considerably narrower scope, perhaps even denoting an empty set, but has been read simply as 'language' by some and 'Universal Grammar' by others. The term 'language instinct', popularized in Pinker (1994), has been rejected equally vehemently (e.g., Tomasello 1995). Frankly, it is unclear to me whether *any* acronym or shorthand version of the 'human capacity to acquire language' will escape a similar rhetorical assassination. Perhaps the field of biolinguistics will have to do without any such term for the time being (although I would personally vote for 'language acquisition capacity' as a relatively neutral designation).

2.3. *'Innate Knowledge'*

A similar terminological morass surrounds the term 'innate', and particularly the concept of 'innate knowledge', although the problems here are at least partly substantive rather than terminological. The deep conceptual problem ultimately stems from the complexity of epigenesis (the complex interaction in the developing organism between developmental programs and the internal and external environment), to be discussed below. But the terminological problem hinges on what we are prepared (or inclined) to call 'knowledge'. Knowledge is prototypically a representational state of adult minds, implemented somehow in their brains. We know enough today to say that this implementation will involve the morphology of individual neurons, their complex interconnections with other neurons, and the computational activities these neural circuits engage in. From this mechanistic perspective, it would be odd to ascribe 'knowledge' to genes, or to the just-fertilized egg. But what about the newborn infant's 'knowledge' of language? Here we are on uncertain ground, for the child is certainly born with a brain, equipped with proclivities to attend preferentially to certain things (like human voices) and not others (like dog barks or engine noises). Even at birth the newborn already expresses preferences for its own mother's voice, or her native language, or a lullaby she sang while the child was still *in utero* (Mills & Melhuish 1974, DeCasper & Fifer 1980, Mehler *et al.* 1988, Hepper 1991, Spence & Freeman 1996) — implying that the fetal environment has already shaped this newborn brain. This constitutes, perhaps, a kind of knowledge. In addition to such rapidly-acquired proclivities, the child manifests constraints on the type of regularities it extracts from linguistic input, and these constraints have been argued by many authors to be important or even necessary components of the child's capacity to acquire language. Do such unconscious proclivities and constraints constitute 'knowledge'?

2.4. 'An Instinct to Learn'

Light can be shed on this question by examining the analogous but better-understood situation in birdsong learning, where an elegant and insightful model of a biologically-based cultural capacity has been developed by Peter Marler. Most songbirds (nearly half of roughly 9,000 bird species) learn their song: A young bird must hear exemplars of the song of its species in order to produce a normal song (Catchpole 1973, Marler & Slabbekoorn 2004). Birds raised in an aviary with other species, but without access to conspecific song, will sing either a completely abnormal song, or (in some cases) will learn the song of another species. Crucially, most birds do not simply mimic the song of adults exactly: In many species, individuals create new, novel songs that are built upon but not identical to the songs they heard as nestlings. This creative aspect of birdsong ensures that each generation hears slightly different songs from those of the previous generation. This process of song transmission across generations, with slight novelties introduced by creativity and or erroneous copying, leads to 'dialects' of birdsong: Birds in different regions sing quite different learned songs. This cultural evolution process can quickly 'repair' song in a population experimentally seeded with aberrant song, correcting it toward the species-typical norm (Fehér *et al.* 2009). But just as a human child of Chinese descent can learn perfect English, a young bird exposed to a different dialect than that of its parents will master the new conspecific dialect.

Equally crucially, young birds exposed to the song of many different species will unerringly hone in on the song of their own species: A songbird appears to be born with a proclivity for the song 'style' of its own species, to which it will attend preferentially. So the bird's propensity to learn is constrained in certain ways: It is not simply a 'general purpose' system that will learn anything it hears. These facts have forced students of birdsong to progress beyond simple-minded nature/nurture dichotomies. Marler's model of birdsong acquisition instead integrates both biological and 'cultural' factors, which are inextricably intertwined in an *"instinct to learn"* (Marler 1991). Songbirds, like human children, are born with a *readiness* to master their species-specific communication system, but they are not born *knowing* this system. Part of this biologically-given readiness is a proclivity to attend to certain types of auditory stimuli (conspecific voices and songs) and not others (dog barking, machine noises, etc). Constraints exist on what can and cannot be learned: There are limits on the sorts of artificial birdsongs a youngster can absorb. These facts show clear parallels with the facts of human language acquisition, and a model of the human cultural capacity as an 'instinct to learn' is an important improvement over currently more popular metaphors. This conceptual model has recently been advanced explicitly to model the acquisition of human language (Doupe & Kuhl 1999, Marler 2000, Okanoya 2002, and Fitch, in press).

Returning, thus equipped, to the term 'innate knowledge', it seems to me somewhat misleading to refer to the constraints on the fledgling bird's song acquisition system as 'knowledge'. These constraints (whatever they might be) are not themselves knowledge but instead influence the knowledge the bird will someday possess. I would make the same terminological caveat, *mutatis mutandis*, about human language acquisition. However, many scholars are perfectly willing to term such innate constraints 'knowledge'. I am happy to accommodate them, so long as the distinctions are kept clear between behaviors that are truly innate (e.g., the acoustic structure of human laughter or cry, and the inborn link between these sounds and pleasure or pain) and those, like speech sounds or birdsongs, for which an innate basis for acquisition exists, but where the behaviors themselves depend on structured environmental input to be acquired and expressed. This distinction illustrates why the term 'language instinct' is misleading. The prototypical cases of instinctual behaviors, such as mammalian crying or suckling, a chick's escape from its shell, or a fly's grooming, really are genetically-coded behaviors, fully-functional at birth. 'Instinct' properly characterizes the child's *acquisition system,* but not the knowledge that system will eventually acquire. We are born with a language acquisition 'instinct' but not language *per se*. Again, the terminology is less important than the crucial underlying principle. What, precisely, is the nature of the capabilities, biases, proclivities and constraints that the human child brings to the problem of language acquisition?

2.5. Beyond Disciplinary Discord

Whenever people vehemently reject a proposition, they do so not because it simply

> *does not recommend itself, but because it does, and yet its acceptance threatens to hamper their thinking in some important way.* (Langer 1942: 238)

To summarize, the current literature on the biology of language reveals a somewhat depressing disciplinary landscape. Despite agreement about the central interest of the questions, and core *explananda*, and the promise of the diverse approaches and perspectives represented, members of competing factions too rarely cite each other or interact constructively. Theoretical discussions are often dominated by rhetorical battles and ideological or terminological debate rather than constructive attempts to make tangible progress. Much of the criticism that currently divides the relevant fields boils down to "My opponent says we should look to *x* for answers, but I believe we should look to *y* instead". Typically, both *x* and *y* are probably important. Given the large number of open questions, biolinguistics will be better off when individual researchers pursue those topics and approaches they believe are important and promising, and refrain from attacking others who have different interests or try different approaches. There is little to be gained from such attacks, and if my experience is any guide, much to be lost.

One can only hope that, whatever else happens, biolinguistics will shed unproductive rhetoric and get serious about making empirical progress. In addition to the stunning progress in contemporary biology, the grounds for optimism within linguistics include increasing convergence among long-separated theoretical approaches to syntax (e.g., minimalism, tree adjoining grammar, construction grammar, and functionalist approaches) towards heavily lexicalized theory of language, with a few basic and powerful operations (e.g., merge, adjoin or unify — see Joshi *et al.* 1991, Stabler 2004). Neighboring fields like neurolinguistics have proven willing to take insights from generative linguistics and test them empirically (Caplan 1987, Friederici *et al.* 2002, Arbib 2005, and Hagoort 2005b), and biolinguistics as a whole will do well to follow this path. Interest in biological approaches to language seems to be growing rapidly in all disciplines, so those established scholars prepared to indulge in self-destructive turf wars should be equally prepared to watch the incoming neuroscientists and biologists take over the field.

3. Beyond Evolutionarios: Testing Biolinguistic Hypotheses

I consider it self-evident that the appropriate models for biolinguistics come from the natural sciences, such as physics in the early twentieth century, and cellular and molecular biology or neuroscience today. Theorists in these fields consider the issues, define their terms, and propose hypotheses that generate testable predictions. Experimentalists implement empirical research programs to test the predictions, based on widely accepted norms of good experimental design (e.g., explicit consideration of, and controls for, alternative hypotheses) and inferential statistics. The historical success of this 'normal science' approach hardly needs emphasizing: Our modern lifestyle from computers and cell phones to agriculture and medicine relies upon it, and the future holds, if anything, an acceleration of progress in understanding the physical and biological world.

There is no reason that theorists and experimentalists should be different individuals, and I think at the present state of play most biolinguists need thorough familiarity with both theory and experiment. This is especially true for evolutionary questions, since generating *testable* predictions is far more difficult than coming up with untestable evolutionary scenarios. 'Evolutionarios' are entertaining but typically offer experimentalists little to work with. Despite the dearth of testable hypotheses, and surfeit of evolutionarios, in current discussions, I think the situation is remediable. The onus is on theory-makers to generate clear definitions of terms and hypotheses, and practically testable hypotheses. Furthermore, progress will be aided by comparing and contrasting *multiple hypotheses*s, not simply rejecting implausible null hypotheses in favor of single pet hypotheses. Ultimately, as for physics, what biolinguistics needs most are creative empirical tests of hypotheses.

Since Darwin, evolutionary biologists have been testing functional and phylogenetic hypotheses quite successfully, despite our lack of time machines, using the *comparative method* (Harvey & Pagel 1991). Although Language, writ large, is unique to our species, many (probably most) of the mechanisms *involved* in language have analogs or homologues in other animals (Hauser *et al.* 2002, Fitch 2005b), and their comparative study thus offers biolinguistics crucial insights. Furthermore, new genetic techniques make it possible to roughly date the origins of mutations (e.g., Enard *et al.* 2002). A combination of a broad comparative approach, molecular genetic techniques, and creative examination of individual differences among humans offers many ways to test evolutionary hypotheses. For example, consider two venerable hypotheses about the origins of human speech.

Scholars have debated for centuries whether the lack of speech in other animals results from peripheral anatomy of the vocal tract (H1), or the nature and structure of the central nervous system (H2).

Recognizing that dolphins were mammals with large brains, Aristotle suggested that their lack of speech results from their lack of loose tongues and lips (Aristotle 350 BCE). Similarly, the discovery by Europeans of the (speechless) apes led to renewed consideration of the crucial capacities underlying speech, and anatomist Peter Camper concluded that the lack of speech in orangutans was caused by their large air sacs (Camper 1779). Both of these ideas are special cases of H1. Other scholars, like Darwin, considered these arguments, but sided with H2, that central neural factors must be critical: "The relation between the continued use of language and the development of the brain, has no doubt been far more important" (Darwin 1871).

3.1. The Descended Larynx

As a modern instantiation of H1, consider the descent of the human larynx (Fitch 2000b). The lowered larynx and tongue root of humans was hypothesized by Philip Lieberman and colleagues (1969) to constitute an adaptation to produce a wider range of speech segments (particularly the point vowels, and the 'supervowel' /i/, used in vocal tract normalization). At that time, and for the next 20 years, both the descended larynx and vocal tract normalization were believed to be uniquely human (Lieberman 1984). In my PhD thesis (Fitch 1994), I developed a related hypothesis, based mainly on principles from physics and physiology, that human formant perception might build upon a capacity for size estimation predating speech, providing a pre-adaptation for the use of formants in speech (H3). This hypothesis required formants to be tied to body size, and clearly predicted that formant perception, and its use in size estimation, would be more widely present in other animals. Thus, it was based on a number of testable assumptions and made numerous testable predictions, and in the last 15 years my colleagues and I have been busy investigating them. We have found that, as predicted, formants provide a reliable cue to body size in many species, because body size, vocal tract length, and formant frequencies are inter-correlated (Fitch 1997, 2000a, Reby & McComb 2003). Further, it predicts that listeners should *use* this potential source of information as an indicator of body size, as several species do (Fitch 1994, Reby *et al.* 2005, Smith *et al.* 2005, Ghazanfar *et al.* 2007). Finally, these finding spurred a closer look at non-human animal vocal production, revealing a descended larynx (once believed uniquely human) in several non-human species (Fitch & Reby 2001, Weissengruber *et al.* 2002, Frey & Riede 2003).

Most of the studies above were directly spurred by specific theoretical questions about the evolution of speech. Besides demonstrating that the descended larynx is not uniquely human, and suggesting that both formant perception and vocal tract normalization build upon primitive mammalian auditory mechanisms, these data revealed that formant signals are an important component of vertebrate communication, are used to judge size, and that these ancient shared uses are still operative in modern humans. They provide abundant evidence consistent with H3, the pre-adaptive hypothesis of Fitch (1994), which thus becomes a serious contender as the original adaptive force driving the descended larynx in our species. Improved speech is no longer the only plausible evolutionary explanation for laryngeal descent, as previously assumed (Lieberman 1984), and it is possible that the descended larynx in adults evolved *before* spoken language.

Equally importantly, these and other recent data on vocal production in mammals demonstrate that the vocal tract is a highly flexible, reconfigurable system: Any mammal can lower its larynx dynamically (Fitch 2000c). Such data offer strong evidence against H1 in its strong forms. While our vocal tract certainly influences the types of sounds we can make, and has presumably been selected in human evolution for its beneficial effects on mechanical control and/or the speed of information transmission (as argued by Lieberman 2006), peripheral anatomy is not a crucial Rubicon that needed to be passed before humans could evolve spoken language. The descended larynx/tongue root is not the core factor keeping chimpanzees from speaking, and by process of elimination, that factor must rest in their brains, not their tongues. The comparative data indicate that neural factors, rather than peripheral anatomy, provide the core mechanistic basis for human speech capacities. What keeps chimpanzees from talking, but allows some seals to talk (Ralls *et al.* 1985) is the configuration of their brains, and not that of their tongues or vocal tracts. But while we have made tangible progress by rejecting the peripheral vocal apparatus as the core factor underlying human speech, this research as yet offers little insight into which aspects of the central nervous system *are* different. Rejecting H1, we tentative accept the alternative hypothesis H2.

3.2. Hypothesis 2: Into the Brain

Any hypothesis based on the idea that it is increased neural control over vocal production that allows humans, and not other primates, to speak must posit some difference in neural circuitry that enables this increased control. Given the complexity of speech, and of motor control, there are likely to be several such differences. One well-documented difference between humans and other primates is that our species possesses *direct connections* from lateral motor regions down to the motor neurons that drive the vocal apparatus, particularly the larynx and diaphragm (Iwatsubo *et al.* 1990, Jürgens 1994). By hypothesis, these connections allow increased voluntary control over the vocal organs, and better coordination between the facial and tongue musculature and phonation (which is crucial to human speech). Of course, although plausible, this 'Kuypers/Jürgens' hypothesis (H4) does not by itself prove anything: There are many small differences between a human and chimpanzee brain, and no guarantee that this one is critical to the known behavioral difference. How could H4 be tested?

The existence of other vertebrates with complex vocal learning open the door to an understanding of the mechanisms of vocal control, at both the neural and genetic levels. Although songbirds are by far the best understood group, mammalian vocal learners include cetaceans, seals (Janik & Slater 1997), bats (Knörnschild *et al.* 2009) and probably elephants (Poole *et al.* 2005). Unfortunately, both birds and tractable cetaceans (e.g., dolphins) have a brain and vocal tract very different from that of humans. Nonetheless, the data from birds are consistent with H4: Birds have direct connections between the telencephalon and the primary motor neurons controlling their phonatory organ, the syrinx. While consistent, this is not perhaps as compelling as we would like.

Among mammals, both seals and bats use a normal mammalian brain to control a normal mammalian vocal tract, and thus provide a unique but mostly untapped source of information into the neural and genetic mechanisms underlying complex vocal control (particularly in phocid seals with complex learned 'song' (Janik & Slater 1997, van Parijs 2003)). Currently, though, most questions one might ask about seal neuro-anatomy and vocal production have a simple answer: Nobody knows, because nobody has looked. The discovery of a species of fruit bats with complex vocal learning is so new that very little is known about neural control in this species (Knörnschild *et al.* 2009). So these are clear, open predictions of the hypothesis, waiting to be tested.

3.3. Convergence, 'Deep Homology', and the Broad Comparative Method

Although the significance of research on birds, bats, deer or seals is sometimes disregarded by those interested in human language because it does not concern primates, and thus does not reveal homologous mechanisms, this attitude misses two crucial points about the comparative method. First, convergent evolution (e.g., of complex vocal imitation in humans, birds, seals and bats) allows us to *test* adaptive hypotheses. In convergent evolution, each clade that has evolved a trait constitutes an independent evolutionary data point. This is not true of a group of species that all inherit a homologous trait from their common ancestor: No matter how many species share it, such a trait constitutes a single data point. This is a fundamental insight of Darwin's use of the comparative method, as well as modern statistics for evolutionary hypothesis testing (Felsenstein 1985, Harvey & Pagel 1991).

A second, more surprising, fact about convergent evolution is much more recent. It follows from a central realization in modern molecular biology concerning the profound *conservation of genetic mechanisms* across disparate living organisms. Genes involved in development turn out to be highly conserved (Gehring & Ikeo 1999, Carroll 2000). Even traits that have evolved *convergently* may often rely upon *homologous* genetic and developmental mechanisms (termed 'deep homology' by Shubin *et al.* 1997). This discovery vastly broadens the scope of the comparative method, which has traditionally focused mainly on homology (though see Gould 1976). The new data pouring in from diverse distantly-related species (especially birds and rodents, but including pufferfish, flies, worms, yeast, and slime molds) reveals a stunning consistency in underlying genetic and developmental mechanisms in this diverse assemblage (Carroll *et al.* 2005). Such underlying conservatism of genetic details was unimaginable two decades ago. Even phenotypic traits that evolved convergently (and are thus homoplastic) often share common developmental and genotypic mechanisms. Therefore, a broad comparative approach that incorporates homoplasy in addition to superficial homology has deep insights to offer. Biologists can avail themselves of a much broader range of species than previously thought, and confidently expect that much of the resulting data will be relevant to human traits (Carroll 2003, Carroll *et al.* 2005). For example, the discovery of mammals with a descended larynx opens the door to genetic and physiological research on the mechanisms underlying this trait. Widespread conservation of developmental mechanisms gives hope (though not certainty) that similar mechanisms may underlie laryngeal descent in humans and in species, like deer, amenable to experimental study.

This story is of course far from over: Replications remain scarce, and further data are clearly needed. While a plausible case can now be made against H1, and for the pre-adaptive hypothesis H3, one might suppose that H3 never could be demonstrated, as these events occurred pre-historically but do not fossilize. Fortunately, this is not true: Comparative molecular biology offers a new and exciting path out of this apparent dead end. If we can uncover the molecular genetic basis for the descended larynx *and* for the complex vocal control underlying speech, we can use the techniques developed by molecular evolutionists (e.g., Enard *et al.* 2002) to date the selective events that established the corresponding alleles during human evolution. If the selective sweep leading to 'laryngeal descent genes' preceded that leading to 'control genes' (in quotes because it is unlikely that the alleles in question function exclusively in these domains), this would be strong evidence against Lieberman's hypothesis that speech preceded (and selected for) the descended larynx (and therefore in favor of the alternative).

In summary, the evolution of speech provides numerous evolutionary hypotheses that can be, and have been, tested. This leads us to a certain amount of optimisim about our ability to move beyond the domains of speech production, and resolve debates about core aspects of language: Syntax and semantics. And it brings us to the first of the 'hard problems' facing biolinguistics.

4. Mind and Brain: The Need for Bridging Theories of Neural Computation

> *Trying to understand perception by studying only neurons is like trying to understand bird flight by studying only feathers.* (Marr 1982: 27)

In his book *Vision*, a foundational work in cognitive science, David Marr argued that progress in understanding the visual brain requires research at multiple levels — including the implementational level (neurons and synapses), the algorithmic strategy used to tackle the problem, and the computational-level description of the problem space itself (Marr 1982). He used Chomsky's goal of formulating a computational model of language (what Chomsky termed a 'competence' model), as an exemplar of this approach. While Marr's multi-level approach has been embraced in the computational neuroscience of vision, its application to language remains relatively unarticulated (though see Poeppel & Embick 2005). I think this results at least partially from a failure in the cognitive sciences to fully embrace the insight that progress will require multiple, complementary levels of description, at the computational, algorithmic *and* implementational levels. Most crucially, we need *bridging theories* that go between levels of description, particularly the computational and algorithmic levels.

4.1. *Multiple Levels of Description*

Despite a long-running debate between connectionists and symbolists in cognitive science (e.g., the many responses to Fodor & Pylyshyn 1988), a connectionist model at the implementational or algorithmic level is not necessarily in conflict with a symbolic computational model, but rather a potential complement to it, as clear thinkers in this debate have remained well aware. But accepting the need for multiple levels of description unfortunately doesn't provide a road map for how to formulate models at each level, or how to link the levels. For that, lacking a general theory of neural computation, we must currently take a catch-as-catch-can approach, using whatever clues we can find. The problem is particularly sharp given that our most powerful empirical tools at the neural level (e.g., single-unit recording or experimental gene regulation) are unavailable for the study of language because the species employed lack language, and the techniques cannot generally be applied to humans. At the highest computational level of language, our best guides must still come from behavioral studies, both psycholinguistics and traditional theoretical linguistics, with some help from brain imaging.

Comparative linguistics and typology are important additional elements, since the study of diverse languages can sharpen our focus on the problem by cataloging the diversity of solutions to it. In a few cases (e.g., metrical phonology and stress systems), linguists have already developed quite sophisticated models that seem capable of encompassing most of the diversity of the world's languages (e.g., B. Hayes 1995): Both the required theoretical primitives (such as syllables, stress, feet, and prosodic words) and generalizations (e.g., the 'iambic/trochaic law'), are relatively clear and uncontroversial. Such aspects of language seem ripe candidates for constructing algorithmic models incorporating psychological data (e.g., Cutler 1996) which can ultimately be translated to models of implementation. Unfortunately, however, such oases of clarity and agreement are the exception in linguistics. Consideration of the diversity of languages allows one to exclude certain possible theories (e.g., a theory that syntactic structure assignment relies necessarily on word order is falsified by 'non-configurational' languages like Warlpiri that have free word order; cf. Austin & Bresnan 1996). However, besides a general agreement on such theoretical primitives as words and sentences, and on the need for structure-dependent rules, there seem precious few specific theoretical claims that are beyond dispute in contemporary syntax or semantics.

4.1.1. The Mechanistic Level

Given that research and discussion at the purely computational level have so far failed to converge, perhaps there are lessons to be learned from considering the lower levels of description. A crucial lesson from computational neuroscience has been that progress typically results not from investigations at a single level of description, but by attempts to bridge between levels: It is the intersection of constraints from the different levels that gives us purchase on the problem (Rolls & Deco 2001). Our theory of color vision is informed by the understanding that there are three types of cones, and our theory of motion detection by the discovery of separate populations of cells interested in motion and not color. Similarly, consideration of neural data may help theoretical linguists 'cleave nature at the joints' in their attempts to discover robust and useful computational primitives in language. Current brain imaging techniques (fMRI, PET) provide little insight into the computation ⇔ algorithm linking problem. Knowing *where* brain activity increases in some language-related task (e.g., generating an inflected verb, or imitating a spoken word) provides pointers about where to look. Similarly, systems that provide high temporal resolution (EEG, MEG) can provide indications of *when* certain neural regions are activated, and thus provide better data for testing causal models of language processing. But both still leave open *what* the actual corresponding computation is: What aspect(s) of the circuit diagram are crucial.

4.1.2. The Search for Computational Primitives

Despite the value of brain imaging techniques, we cannot expect them to solve the central problem. For that, we need to distill what we know from linguistic theory into a set of computational primitives, and try to link them with models and specific principles of neural computation. Unfortunately, appeal to general computational principles may be of limited value. To the extent that vision is best conceptualized as a 'bag of tricks', where each aspect of vision (color, motion, depth perception, etc) has its own unique solutions, there may be no general conclusions available about computations underlying 'vision' in general. The same may be true of 'language'. However, vision is a far more ancient evolved system than language, so this lesson may not generalize, and certain classes of models seem to pop up consistently. Individual neurons are slow and sloppy, and sometimes die, and these basic facts have often led to the evolution of parallel redundant circuits, rather than circuits that seem optimal to electrical engineers who have fast, precise and reliable computing elements available.

This difference between silicon and cell-based computers has led to abstract notions of 'natural computation' (Richards 1988, Ballard 1999) that may hold useful clues for biolinguists building bridges between the algorithmic and computational levels. While a focus on just the computational level ('competence') remains a necessity in everyday work, consideration of 'performance models' (including both algorithmic psychological models and, implementational neural models) should ultimately inform our debates about 'natural' theoretical primitives (Fitch 2005a, Hagoort 2005a, Friederici *et al.* 2006). Thus we need linguistic models that are explicit about the computational primitives (structures and operations) they require, and that attempt to define linguistic problems at a fine enough grain that one can discuss algorithmic and implementational approaches to their solution. We need a list of computations that linguistic theorists deem indispensable to solve their particular problem (e.g., in phonology, syntax, or semantics).

4.2. A Tentative List of Computational Primitives

A non-exhaustive smorgasbord of linguistic computational primitives, based on my reading of the linguistic literature, may help make my point, illustrating the sort of computational structures and operations that any model of language will need to incorporate. While different theorists might give rather different names to them (e.g., Jackendoff 2002), or object to my overly schematic descriptions, experts can hopefully read between the lines to see what I'm getting at. Alternatively, my list may spur the theoretically-inclined reader to generate their own, quite different, list of primitives. This list simply illustrates by example the sort breakdown needed to begin building bridges between computational theories, and the algorithmic and implementational levels.

(1) Phonology and Syntax: Data structures including trees and related multi-level structures are needed, as are structure-building algorithms that concatenate constituents into tree structures, perhaps by forming temporary links among smaller structures stored in long-term memory (the 'Lexicon'); evolutionary links with motor control seem likely.

(2) Phonology: 'Natural classes' of phonemes, such as stops or high vowels, are required because many phonological phenomena apply to specific classes (rather than specific isolated phonemes, or broader class such as vowels); evolutionarily, such natural classes may have built upon more general auditory categorization circuits.

(3) Syntax (structure-dependent rules): Computations that apply to classes of structures (noun phrases or sentences) rather than specific words or broad types such as nouns.

(4) Syntax and Semantics: Dependencies between words require the equivalent of variables or subscripts that can bind constituents into temporary linkages, such as article agreement, anaphora (binding pronouns to whole noun phrases, in the simplest case), or topic/comment markers in connected discourse.

(5) Semantics (thematic roles): Distinctions like agent vs. patient are necessary to distinguish the roles of multiple actors in such propositions as 'John likes Mary' vs. 'Mary likes John'; although English does this mainly with word order, many languages have more flexible ways of marking and expressing this key semantic difference (e.g., case-marking).

(6) Semantics: Complex conceptual structures, built up with embedders, conjunctions, and disjunctions with scope, are needed and combining primitive predicates into larger complexes, with possible attribution of an external referent, or truth or falsity, to the whole complex, is a crucial computation in linguistic thought; despite considerable disagreement about whether this computational capacity is part of syntax, semantics or more general conceptual abilities, there is little disagreement about its basic necessity for both language and other aspects of complex thought.

4.3. Examples of Bridging Constructs

I will focus on the algorithmic ⇔ computational bridge in biolinguistics because we clearly have substantial work to do in attempting to build this specific set of bridges. The good news concerning the other, algorithmic ⇔ implementational bridge is that there is little evidence suggesting that language involves any major discontinuities from other aspects of cognition at low implementational levels. The neocortical circuits involved in language have the same layered arrangement as other non-language circuits, are connected with subcortical systems like thalamus, basal ganglia and cerebellum in the same ways, and use the same types of cells releasing the same neurotransmitters with the same kinds of action potentials. The developmental processes by which these circuits arise follow the same basic principles as the circuits involved in vision or motor control in diverse mammals (Finlay & Darlington 1995). Whatever implementational details differentiate language from other cognitive functions, they appear to be only rather subtly different from those underlying other aspects of cognition. Thus we can confidently expect that most aspects of language implementation will be based on more general principles of brain development and function, and that good first-order approximations can be built upon shared principles of neural computation (Ballard 1999, Rolls & Deco 2001). We can also expect that such first-try models will uncover some important differences in the details (otherwise, *all* brains, including those of other species, would be able to compute language readily), but these will not rely on wholly new neurophysiology or connectivity. For this reason, I see the algorithmic specification of the various components of language, based upon explicitly stated computational primitives and algorithm models, as a crucial missing link in our attempts to build the larger bridge between mind and brain. For a similar argument see (Poeppel & Embick 2005).

4.3.1. Tree Networks and Algorithms over Trees

To illustrate how a computational primitive might be fleshed out at the algorithmic and neural levels, consider the first computational primitive: Linking trees into larger complexes. First, because tree abstractions appear to be ubiquitous in theoretical models of cognitive phenomena (Simon 1962), not just language, research in other cognitive domains (e.g., chess playing, music perception, object recognition, or motor control) may offer insights into the nature of linguistic trees. Second, since words have a hierarchical internal structure (Kenstowicz 1994), and can be thought of as memorized chunks of structure, the processes by which words are learned, stored and recalled should have much in common with other aspects of long-term memory. Once recalled, such 'treelets' must be temporarily combined into larger structures via some process of binding (either adding a treelet's root to the twig of the larger tree, and thus preserving tree structure topologically, or binding two twigs to create 'tree networks'). This process may inherit aspects of the process whereby automatized motor subroutines are combined into temporary motor plans as we execute complex novel actions (e.g., Lieberman 1998b, Arbib 2005). In the same way that our ongoing plans are sometime interrupted and demand a reconfigured plan, the linguistic tree we have built during an ongoing parse may need to be abandoned and reconfigured (e.g., in garden path sentences). Thus, 'performance' theories about how linguistic trees are stored, recalled and recombined may profit from our pre-existing understanding of the neural basis of memory, motor control and other cognitive domains (as envisioned in Miller & Chomsky 1963).

At a more abstract level, such implementation-informed theoretical constructs could have important implications for how we formulate our overall theory. For instance, if we conceptualize language as a whole as a system that maps between high-dimensional conceptual structures ('thoughts') onto low-dimensional signal structures (phonetically-realized speech or sign streams) it immediately becomes clear that this is an ill-posed problem in the technical sense that there can be no unique solution to the signal ⇒ concept expansion problem (due to the greater dimensionality of the target domain), nor perfect solution to the concept ⇒ signal compression problem (there being multiple candidate mappings, each omitting something). There can't be enough data in the signal to allow perfect reconstruction of the original thought structure. Given this ill-posed problem, what is remarkable is that language works so well for communication, and that (in general) we succeed at expressing our thoughts in words, and in reconstructing others' thoughts from their words. The solution demands a massive quantity of shared world knowledge: Far more information is generated by 'reading between the lines' than is literally present in the signal. Pragmatic inference using shared world knowledge is a computational necessity (Sperber & Wilson 1986).

4.3.2. *Evaluating Optimality*

Syntacticians have long recognized that one aspect of the signal ⇔ meaning mapping process is an element of cyclicity in the application of syntactic rules (Miller & Chomsky 1963). Beyond a certain point of expansion, we become unable to deal with large structures and loose ends dangling: We must 'close' or complete old structures if we are to cope with new ones. The first question one can ask is why this effect occurs at all. One likely answer might be that memory limitations ('performance constraints') simply prevent us from what would otherwise be an optimal solution (in much the same way that many theorists agree that memory limitations prevent easy parsing of arbitrarily center-embedded sentences). But an alternative answer is that the nature of the concept-signal mapping problem makes cyclicity a computational necessity: Even an ideal model would include cyclic application of mapping rather than an 'all-at-once' compression. Both models are logically plausible, and adjudicating between them would require two idealized models with which to compare actual human performance. Contemporary computational linguistic parsers don't provide such a model, because they assign syntactic structures, *not* conceptual structures, to strings. Indeed, mapping strings to concepts remains the major unsolved problem in computer language processing (see below). Thus, contemporary linguistics still lacks an 'ideal communicator' model comparable to 'ideal observer' models in vision, and only once we have such models can we decide whether actual human performance on this task is sadly sub-par, due to memory or processing limitations, or in fact are nearly optimal.

5. Genes, Bodies and Brains: Biology Comes to Grips with Epigenesis

Another core issue that faces biolinguistics, and biology in general, is development. How can a single cell (the fertilized egg), with two copies of a few gigabytes of DNA, contain within itself the basis for a newborn's body with 100 trillion cells and a brain with a trillion synapses? How can 25,000 genes possibly possess enough information to specify this process? Alternatively, how could the environment *in utero* provide this information? How could evolution have encoded it? Where does all this information come from?

5.1. Three Reductios of Naïve Models

Let us first dispense with the obvious possible answers in a series of simple arguments, each a *reductio ad absurdum* of the corresponding oversimplistic models, by considering the information available for pure nativist or empiricist models more closely.

5.1.1. The Naïve Nativist Model

The human brain is estimated to contain roughly 100 billion = 10^{11} cells, each of which has between 100 and 10,000 synapses, leading to at least 10^{14} synapses in the brain. To specify 1 of 10^{11} cells exactly, you need 37 bits. Therefore, to specify simply the connecting cell corresponding to each synapse you would need 37 x 10^{14} bits (and to specify the synaptic weight you would need at least eight bits per synapse). There are about 3 billion (3 x 10^{9}) base pairs in mammalian genome, so even if the genome was fully dedicated to specifying brain structure (which it is not) and had perfect coding in an information-theoretic sense, we would have a shortfall of at least 5 orders of magnitude to specify the connections in a human brain: We have 1/10,000th of the DNA we would need to code the detailed wiring of our brains. This 'gene shortage' has led scholars like Paul Ehrlich to conclude that little of our behavior could possibly be innate (Ehrlich 2002). Let us therefore similarly consider an exclusive role for the environment.

5.1.2. The Naïve Empiricist Model

Let us optimistically suppose that we learn something from our environments every second, waking or asleep, of our lives. There are 31 million seconds in a year (3.15 x 10^{7}). If we live to 100, that's just 3 x 10^{9} seconds (roughly the number of base pairs in the genome). The first five years of life, when most language learning is occurring, contain only 15 x 10^{7} seconds. Even the most fortunate and well-stimulated baby has this paltry number of environmental inputs available to specify 10^{14} synapses. Although we can hope that many synapses are influenced by each environmental input, this doesn't help unless each input event, is very highly structured, carrying a large amount of optimally coded information. This seems optimistic, to say the least. Thus the naïve empiricist faces the same vast information shortfall as the naïve nativist.

5.1.3. The Naïve Evolutionist Model

Finally, for completeness, consider the plight of a different type of nativist: An idealized 'evolutionary empiricist' who suggests that natural selection alone has programmed behavior. Vertebrate evolution has occupied about a billion (10^{9}) years. If we optimistically hypothesize (e.g., Worden 1995) a few bits of information per generation to accumulate, that's only a few billion bits again (and of course any particularities of the human brain have had far less time — roughly, 6 x 10^{6} years — to accumulate). Again a vast information shortfall exists, of roughly the same order: This one a shortage of evolutionary time.

Are we to conclude from this little exercise that development is impossible? Or that the evolution of the brain could not have occurred? No, such basic considerations force us to reject overly simplistic models, and to conclude that both the naïve nativist (genome as blueprint) and naïve empiricist/evolutionist (environment as instructor) viewpoints are woefully inadequate models. Such considerations quickly lead all serious thinkers on these problems to realize that understanding any aspect of development and evolution requires understanding the *interactions* between DNA and the world beyond the cell nucleus. Despite its tiresome persistence, 'nature *versus* nurture' is a sterile conceptual dead-end, and any valid answer must consider 'nature *via* nurture' in some form or other (Ridley 2003).

5.2. *Respect for the Cell*

An important new insight in our understanding of how genes build bodies and brains is the central role of *cell biology* in all aspects of development (Kirschner & Gerhart 1998, 2005). Crucially, the trillions of cells in our body break down into only 200-odd cell types, and there are only roughly 25 morphologically distinct cell types in the cerebral cortex. What the genome carries is not instructions for individual cells, but instructions for *cell types*. Furthermore, most of the basic behavior of these cells is shared among all cells in the body (as well as with free-living single celled organisms like an amoeba or yeast), so something like half of our genome deals simply with basic cellular behavior, and only the *differences* from this 'average' cell need to be further specified (e.g., proteins like hemoglobin that are expressed only in blood cells). Each of the many trillion cells in our body is a semi-independent living thing: Under optimal tissue-culture conditions individual human cells can live for years on their own. This is not surprising when you consider that the first two billion years of evolution took place at the single-cell level. Since single-celled organisms have much shorter generation times than multicellular organisms, *most of our ancestors were free-living single-celled organisms*. From this long evolutionary history, each of our cells inherits some rather impressive behavioral capabilities. Each cell contains a complete copy of the DNA of the organism of which it is a part: It carries the entire 'recipe book' for the body along with it. Cells may make epic migrations through the body, following gradients of nutrients and responding to signals left behind by earlier pioneers, and each must eventually find a home and a job in order to survive. Individual cells are highly responsive and adaptable, and can deal successfully with evolutionarily novel circumstances (e.g., finding themselves in a damaged brain or mutant limb).

Once we recognize cells as active, adaptive, information-processing entities, we see that they form a crucial intervening level of explanation between the genetic and whole-organism levels. The apparent paradox of genetic and environmental information dissolves. Sewell Wright already recognized this in 1931: "From the view that structure is never inherited as such, but merely types of adaptive cell behavior which lead to particular structures under particular conditions, the difficulty to a considerable extent disappears" (Wright 1931: 147). The technical details allowing us to flesh out this basic insight have only recently become clear. From a genetic viewpoint, much of the overall complexity of organisms arises through local interactions between cells and their immediate organism-internal environments: The genome doesn't need to specify the shape of a human hand or a bats wing, but simply must constrain the overall pattern of development of a mammalian limb, in a sense 'sculpting' a pre-existing developmental archetype rather than building an iconic 'blueprint' of the final structure (Goodwin & Trainor 1983). As often correctly emphasized (e.g., Dawkins 1986, Ridley 2003), the genome is nothing like a blueprint. It is more like a recipe or program. Like any recipe, it leaves a lot of detail unspecified, and up to individual cells' 'decisions' based on their particular history and circumstances. From an evolutionary viewpoint, there is no need for natural selection to perform a detailed and complete hill-climbing process through a complex, mostly non-adaptive morphogenetic space: It can let robust developmental processes do much of the work. Natural selection simply 'chooses' among the various relatively worse or better-formed, but still functional, options that result from development. This perspective on cells as prime movers in development and evolution is nicely described, with many examples, in (Kirschner & Gerhart 2005), and many of the molecular developmental mechanisms explicated in (Gilbert 2003, Carroll *et al.* 2005).

5.3. *Epigenesis*

Thus, in a way we are finally beginning to understand, recipes for building bodies are constrained both by the information in our genomes and the separately inherited cellular machinery acting on this information. Equally, development is constrained and informed by the environment, and has been shaped by evolution to respond robustly to it. Despite the apparent shortfall of information in any one of the relevant domains, the reality of *epigenesis* — the close interaction between information in the developmental 'program' and information stored in the environment — is that such interaction is fully adequate to specify bodies along with brains and behavior as special cases (Gottlieb 1992). Environmental stimulation, and even social interactions, turn genes on and off, and development occurs via successive waves of interactions among cells, and between cells and their local environments within the body (themselves structured by previous such interactions). Crucially, the relevant 'environmental information' in epigenetic interaction is mostly the *local environment surrounding each cell*, and *not* that in organism-external world. This local environment has traditionally been left out of both nativist and empiricist models, but is clearly where the action is in development, filling in the information shortfall described above.

Each of the trillion cells in our body or the billion cells in our brain has its own, rather myopic, local environment which informs its DNA regulation and thus developmental decisions. Each second of development, different local environments are separately effecting each cell in our body in parallel. While this local internal environment is, for the most part, dependent upon past decisions made by neighboring and predecessor cells, it is also often influenced in important ways by the organism-external environment. This influence is perhaps most marked in the brain (which is the organ most specialized to process organism-external information), but other systems like the immune system have a similarly rich external-responsiveness.

Epigenetic, interactive developmental models are nothing new: The concept has been standard in embryology for many years (Waddington 1957). Experimental embryologists like Spemann recognized that cells respond to messages generated by other cells, and that this determines their fate later in development. Huge advances in our understanding of the genetic basis of development in the last decades have brought such ideas to fruition, and now the molecular basis of Spemann's 'organizer' signal, and many other similar cell-cell signaling systems, is becoming clear (see Gilbert 2003). The mechanisms by which DNA expression is regulated, both in classic epigenesis via transcription factors (proteins that bind to DNA), and longer-term changes (e.g., the new epigenetics of 'genetic imprinting' that can span generations) are now becoming clear (Reik 2007). This progress in turn has led to the construction of new bridges between evolution and development — *evolutionary developmental biology* or 'evo-devo' — which promise to finally close the most crucial remaining gap in our understanding of biology (for authoritative introductions see Carroll 2005, Carroll *et al.* 2005). Today's biolinguists can help themselves to some well-developed models of epigenesis, and how development interacts with evolution, before trying their hand at understanding the epigenesis of language. For further implications of this perspective on the evolution of mind see Fitch (2008).

5.4. *Neurons: A Very Special Cell Class*

This cell-based epigenetic perspective, a central tenet of the evo–devo revolution, is as applicable to the development of brains as to the rest of the body. However, neurons are unusual in a number of ways. The most important is that they are specialized for information processing by networks of neurons, over and above the normal cell-cell interactions that influence all cells. In the case of a neuron in the developing brain, 'finding a job' means taking part in a circuit that behaves coherently, and many of the neurons that are born fail to achieve this goal, and undergo programmed cell death as a result. While the primary constraints on a skeletal cell in a developing bone are physical forces (stresses and strains), for a neuron the relevant forces are the complex ebbs and flows of an 'information economy' established by myriad surrounding cells (both neurons and glia) as well as quite distant neurons influencing it through their axonal projections. Thus the local environment of the brain is unusual both in the type of commodity processed (information) and the topology of interactions (including precise long-distance connections, made possible by the unusually elongated neuronal morphology). While there is every reason to believe that insights from the development of limbs or the lung will carry over to the brain, we can also be certain that new principles are involved in brain development and evolution (Striedter 2004).

5.5. *The Way Forward*

> *One of the principal objects of theoretical research in any department of knowledge is to find the point of view from which the subject appears in its greatest simplicity.*
>
> (J. Willard Gibbs)

The revolution underway in developmental biology has important implications for biolinguistics. Anyone interested in understanding the biological basis for human language acquisition must be prepared to jettison simplistic debates about nature vs. nurture, and unhelpful notions of heritability from old-school genetics ("Dyslexia has a heritability of 45%"). Instead we can expect highly complex interactions between cells of different types, and in different brain regions, to provide the link between genetic changes and individual phenotypes. We can expect few if any cellular behaviours or cell signaling molecules that are qualitatively novel, either to our species or to language (Hill & Walsh 2005), but instead seek combinations of conserved cell processes building neural circuits that perform qualitatively novel classes of computation (Szathmáry 2001). We can expect that such circuits, built of 'normal' neurons using standard neurotransmitters, will exhibit properties and connections that are 'standard' in the mammalian brain (e.g., cortico-thalamic loops), but that these same circuits may show patterns of connectivity that are unusual, and perhaps in some cases unique, to our species or to language itself.

It would be hard to overstate the difficulties we face in discovering such subtle implementational differences. Despite a long history of trying (e.g., Braitenberg 1977), even circuits whose structure is already known in detail (e.g., in the hippocampus or cerebellum) have proved remarkably resistant to abstract computational analysis. Although a variety of simple models of memory or motor control exist, computational neuroscientists have yet to converge on models that are adequately comprehensive yet simple enough to understand. And these systems are broadly shared with well-studied 'model' animal species (mice, rats, monkeys, etc).

Integrating our computational and developmental problems, we can expect that *any* simple developmental model of the key neural computations involved language will be incorrect in its details. Nonetheless, progress will be fastest if we attempt to develop explicit simple models of various language mechanisms, amenable to experimental disproof, and then let the data show us where they are wrong. In the same way that Galileo and Newton achieved huge gains in physics by abstracting away from the existence of friction, we may expect that abstract models of neurolinguistic function and development, based on known aspects of neurophysiology and neural development but tailored to the specific computational needs of language, will offer hope of rapid progress. Progress requires posing simple (perhaps over-simplified) models, knowing they will be wrong, and letting the data tell us *where* they are wrong. As Einstein advised, "everything should be as simple as possible, but not simpler", and falsifiable, simple models will be vastly preferable to complex, unfalsifiable models with too many unconstrained variables.

6. Information and Meaning: The Final Frontier

I will end with a brief look at the aspect of language that I think promises to be most difficult to solve: The problem of meaning. While we have a powerful and well-understood theory of *information,* we still lack a mathematical theory of *meaning*, and developing such a theory poses some knotty conceptual and computational problems. Here, more than anywhere else in this article, I attempt only to point out the problems, without offering even sketches of solutions. I think the magnitude of the problem often (or even typically) goes unnoticed in linguistics, where theorists tend to rely on an already-linguistic conception of semantics (a 'language of thought' of some sort) without focusing on the far deeper difficulties for modeling non-linguistic concepts (cf. Millikan 1987). The last thirty years of animal cognition research leaves little doubt that non-linguistic animals *have* complex concepts and can reason with these, and in general can have rich, active mental lives — despite their inability to express their thoughts to others (Vauclair 1996, Hauser 2000, Griffin 2001, Hurford 2007). These cognitive systems predated language, and form the cognitive foundation for word and sentence meanings today. Thus the problems involved in developing an adequate theory of meaning are very broad, and extend far beyond the confines of language or linguistics. Indeed many of the problems have been recognized most clearly in artificial intelligence and robotics, where attempts to build computers that can execute simple but novel motor acts, recognize objects, or recognize basic referents and thus implement even the roughest approximation to 'meaning' have thus far been relative failures. Some of the key missing ingredients of a rich cognitive theory of meaning include a sub-theory of context, and a theory of relevance.

6.1. Shannon Information as a Foundation

Claude Shannon's formalization of 'information' as a quantifiable mathematical entity was a bold, unifying theoretical move, recognized as revolutionary almost immediately upon its publication (Shannon & Weaver 1949). The success of information theory in the domain of technology would be hard to overstate: This formalization was the basis for all subsequent work on digital representation and communication theory, without which today's digital world would be unthinkable, where virtually all communicated material (text, speech, music, images, video and other data) is rendered as a pattern of bits. Shannon's paper introduced the very term 'bit' and the underlying conceptual framework of the digital revolution. Shannon's 'information' was also recognized as deeply interesting theoretically, because its intimate formal connection with the physical concept of entropy offers a link between the inanimate world of particles and probabilities, and the biologically critical worlds of information and meaning. However, Shannon and co-inventor Norbert Wiener both clearly recognized that the revolution they sparked was only partial, because 'information' in this formalization is far from identical with information as normally understood. In particular, Shannon and his popularizer Weaver were both explicit in 1949 that Shannon information fails to incorporate any notion of the *meaning* of a signal. This limitation leads to some non-intuitive propositions in information theory (e.g., that the 'information' in white noise is greater than that in a symphony or speech). Despite Shannon's own clarity on the limitations of 'information' in his sense, this caveat has been largely ignored on two important fronts. From a practical viewpoint the distinction between meaning and information has become blurred (e.g., in engineering), and from a theoretical viewpoint Shannon's call for an extension of his concepts into the domain of true, biologically-relevant meaning has gone unanswered (e.g., in cognitive science or neuroscience).

Although its incompleteness has periodically led to a call to abandon Shannon information theory entirely (e.g., King 2004), this would be unwise given the manifest success of this theory in all domains to which it has been earnestly applied (both technology and neuroscience), along with the steady improvements in the theory (MacKay 2003). Thus, I think the goal for an eventual theory of meaning should be to build upon Shannon's formalism, incorporating his theorems and extending them. I suggest that two key desiderata for such an extended theory of information, incorporating meaning, are formalizations of context and of relevance.

6.2. Context and Relevance — 'One Man's Signal is Another Man's Noise'

The same signal may be meaningful in one context and meaningless, or meaningful but irrelevant, in another. At several levels this context-dependence is captured by the phrase quoted above. Meaning must be defined relative to some *context*: A broad temporal-spatial window of data, both organism-internal and -external, much larger than the signal whose information is to be interpreted. This context, provides the data relative to which the meaning of any signal is interpreted. A signal (e.g., white noise) may have a meaning of 0, despite its information-rich high bit rate. This distinction may help to resolve the non-intuitive nature of Shannon information: A signal could have high information and low meaning, or lower information (e.g., speech or music, which are quite redundant) and high meaning. *Relevance*, a basic quantity in any adequate formal theory of pragmatics (Sperber & Wilson 1986), depends not just on current external context, but also on an individual's current cognitive state: Drives, goals, unanswered questions, hypotheses being processed. Relevance is thus in the eye of the beholder, and demands a formalization of external context *and* goal-directed internal context.

We should in principle be able to define ideal observer ('ideal interpreter') models that can extract all the possible connections between all possible signals for a given world and goal context. Unfortunately, the well-known combinatorial explosion that results poses serious obstacles to using such models to control action, because a set of computations subject to unconstrained combinatorial explosion is of little use in real-time computation of meaning. This is the infamous 'frame problem' in artificial intelligence (Ford & Pylyshyn 1996), and the 'solutions' to the frame problem currently on offer in AI all essentially involve *a priori* limits on the extent of this explosion: All variants of what Simon long ago dubbed 'bounded rationality' (Simon 1957), or of Chomsky's innate biases. However, it is unclear that such bounded models can do justice to the seemingly unfettered connection-finding revealed by individual human linguistic creativity, or of the social ramifications of this creativity, as seen both in culture and science. While discussions of the frame problem in technology have grown less central as various work-arounds have been developed, the central epistemological issue in understanding the mind is not solved, or even obviously confronted, by such 'solutions' (for discussion see Fodor 2000: Chap. 2). Further, no ideal interpreter model alone can capture the relevance of a signal without an additional specification of goals, problem states, current behavioural sequence, current location, etc. There is a considerable amount of explicit computational theory still missing here.

6.3. The Future: Comparative Cognition Meets Formal Semantics?

Given the problems context-dependent combinatorial explosion causes for contemporary computers and robots, the remarkable fact is that organisms seem to rarely suffer from the frame problem. Indeed, simple motor tasks that seem trivial to us (or to a monkey or a dog) — locomoting around obstacles, negotiating novel paths successfully, or picking up objects without breaking them — remain daunting for today's robots. At the level of perception, perceptual 'mistakes' like illusions are the exception and not the rule, and we seem quite effortlessly to exclude a huge variety of possible interpretations, converging reliably on a relatively accurate but extremely flexible model of the world — again a trick that evades today's best machines and algorithms. In computational linguistics, even simple sentences generate hundreds of possible parses — but we humans rarely even consider more than one of them. One thing that seems common to many of these feats is our ability to use context of various sorts to prune away all but the most probable branches of the tree of possibilities. Our ability to evaluate the relevance of various possible interpretations builds on this more basic context-dependence to explore models of the future or possible worlds. Almost all of this computational generation and pruning is unconscious (perhaps necessarily so, as I have argued in Fitch 2005a, 2008). Furthermore, most of these processing capabilities must have predated the evolution of language, since effortless incorporation of context in decisions of relevance typifies the behavior of a dog or chimpanzee as much as a human. Thus, in some sense, the conceptual and neural basis of 'meaning' is a more basic problem than, and its solution should be logically prior to, an understanding of semantics in natural language. Thus, unfortunately, a general theory of 'meaning' ultimately demands a complete theory of how brains make minds, clearly one of the hardest problems left for science to solve. Ultimately, I believe that new theoretical tools will be necessary to understand meaning in the more general non-linguistic sense I have been discussing, and that the study and modeling of non-linguistic animal cognition will play a crucial role in such an enterprise. For now, an attack on the problem from multiple (hopefully someday converging) perspectives will be required.

Linguistics, in the guise of formal semantics, potentially has something to offer this enterprise. Contemporary semanticists have developed a rather powerful set of theories and formalisms, with truth-value, possible word, and model-theoretic semantics among the prominent theoretical approaches, and a variety of formalisms based upon propositional and predicate calculus and their extensions (Portner 2005). Such approaches are unlikely to solve some of the deeper problems of an embodied (organism-dependent) and context-dependent theory of meaning, precisely because they intentionally abstract away from such problems (see e.g., Montague 1974). Nonetheless, the tools provided by formal semantics should play an important role in our final understanding of linguistic semantics by providing rigorous definitions of the sorts of problems that must be solved (e.g., logical entailment or scope of quantifiers). Contemporary semantics appears largely to take for granted the existence of non-linguistic models of the world (though work on spatial language provides a welcome, if narrowly circumscribed exception: Landau & Gleitman 1985, Landau & Jackendoff 1993). But real progress in understanding this extra-linguistic context- and relevance-sensitive domain of basic cognition will require considerably more work in this direction, (cf. Jackendoff 2002). Until a well-developed, mathematically-formalized cognitive theory of meaning, applicable to animal cognition and including basic reference and context-dependent relevance, is available, any biologically-based theory of language will remain incomplete.

7. Conclusions and Some Outstanding Biolinguistic Questions, Framed as Testable Hypotheses

With these prolegomena, I have tried to clarify some core problems that face the new science of biolinguistics. The sociological problems discussed at the outset should be soluble with good-will, mutual respect, and self-imposed restraint. Sober biolinguists will recognize that the core problems facing this field are far too big for any one individual to solve on their own (if only because mastery of all the relevant disciplines is impossible for even the most gifted polymath), and will team up to solve them together. I am thus guardedly optimistic that the fascination of the questions and exciting promise of new techniques and approaches will sweep away many traditional barriers to success.

In contrast, the three problem areas that form the heart of this article pose serious scientific challenges. Each is daunting in its own right. When these challenges are combined, it becomes clear that developing a biological understanding of human language is one of, if not the, most difficult problems in all of contemporary science. Although I have tried where possible to indicate possible solutions to at least some aspects of the problems discussed, my primary motivation in this article was simply to clarify the problems themselves. I think that all researchers interested in biolinguistics can profit from musing over these difficulties, and trying to clarify their nature. At the very least, a meditation on the gravity and breadth of these problems can induce a humility about one's own attempts at solutions, perhaps contributing somewhat towards remediation of the sociological problems that hinder the field. But in any case, a clear understanding and statement of unsolved problems is the best spur to their solution.

I emphasized above that the model for progress in biolinguistics will be empirical testing of theoretical predictions, along the lines of physics or molecular biology. Thus I end this article by taking a dose of my own proposed medicine, recapping one testable hypothesis and presenting six more, spanning the range of the problem spaces discussed in this article. Hypothesis (A) below is recapped from section 3, as a reminder of the type of multifaceted research program that we will need to find answers to *any* of these questions. I imagine key contributions by researchers in disciplines as diverse as field and laboratory ethology, theoretical, comparative and historical linguistics, developmental biology and psychology, molecular genetics, experimental psychology, computational linguistics, comparative neuroanatomy, sociology and brain imaging. I will make no attempt to flesh out the theoretical underpinnings of these hypotheses, or to detail the experiments that would be involved in testing them. These are left as an exercise to the reader, as a prolegomenon is best summed up with questions, rather than answers. While these questions don't begin to exhaust the list of testable hypotheses in biolinguistics, I hope they give some sense of the potential interest, breadth and promise of this nascent field, and illustrate the future need for broad and productive interdisciplinary collaboration.

(A) *Speech Followed Laryngeal Descent*

If size exaggeration was a pre-adaptation for speech (Fitch 2002), human genes controlling male pubertal laryngeal descent should have fixated before those involved in complex vocal control (Hypothesis H3, section 3 above).

(B) *Speech Entails Babbling*

If 'closing the loop' between production and perception is a prerequisite for complex vocal learning, all vocal learning species should normally babble (show an early stage of autostimulatory vocal play, e.g., sub-song in birds; Fitch 2006a, 2006b); untested species include pinnipeds, bats, cetaceans.

(C) *Signal Imitation*

If vocal and visuomanual imitation both reflect an abstract domain-general capacity for 'mimesis' (Donald 1991), auditory and visual imitation abilities in individual humans should be closely correlated; if they reflect independent, separately-evolved mechanisms there should be no such correlation.

(D) *Syntactic Power*

If human sentence-parsing capacities indeed occupy the mildly-context sensitive level of the formal language hierarchy (Joshi *et al.* 1991, Stabler 2004), the additional form of memory involved in processing grammars beyond the finite-state level should have the characteristics of a queue, rather than a stack.

(E) *Language Acquisition*

If human language acquisition is just a special case of a general innate capacity for acquiring culture (Tomasello 1999), then individual children's progress in acquiring language should be closely correlated, both temporally and across individuals, with their progress in other aspects of socialization and mastery of non-linguistic culture (cf. Markson & Bloom 1997).

(F) Semantics and Neuronal Arborization

If natural language has cognitive access to conceptual mechanisms that are encapsulated in other species (e.g., chimpanzees), populations or subclasses of neurons with broadened dendritic or axonal arbors should quantitatively distinguish our brains from a chimpanzee brain, and these arbors should be widely distributed throughout the brain rather than restricted to traditional 'language' areas (cf. Enard *et al.* 2009).

(G) Plasticity of 'Critical Periods'

If epigenetic interaction between genes and external environment plays a key role in developing the neural circuits underlying language (Bates 1999), 'sensitive periods' (Lenneberg 1967) during which such interactions are possible should be plastic; in particular, some classes of extreme environmental change (e.g., adoption) should be capable of 'resetting' the language acquisition system in young enough children, with a concomitant change in gene expression patterns in the child's brain — this should not be true of epigenetic processes dependent only on the early-developing organism-internal environment.

One could easily generate many more such hypotheses. The difficulties lie not in hypothesis generation but in developing empirical research programmes to test such ideas. If the current essay helps current and future workers in this new field reject, or confirm, any one of these hypotheses, I would be very pleased.

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