Biolinguistics: forays into human cognitive biology

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Summary - *The present article surveys the field of biolinguistics. It revisits the roots of the field's core research agenda, then turns to the various factors that led to its recent re-emergence, and finally offers suggestions for future inquiry. The essay also serves to highlight certain conceptual issues that should be addressed if the field is to bear its interdisciplinary fruits.*

Introduction

Biolinguistics refers to a branch of the cognitive sciences that focuses on uncovering the biological underpinnings of the human capacity to acquire at least one natural language. As such, and despite its name, it departs sharply from the many subdisciplines of linguistics, which focus on how human languages are put to use in various socio-cultural contexts. That such uses require a (possibly complex and multi-faceted) biological foundation cannot be seriously put into doubt, and biolinguistics takes that fundamental aspect of human biology as its subject matter.

The biolinguistic enterprise grew out of the concerted efforts of several individuals, most notably Noam Chomsky and Eric Lenneberg, in the 1950s to overcome the overwhelmingly behaviorist framework dominating psychology and linguistics in the USA at the time. Although the term 'biolinguistics' did not emerge in its current sense until the 1970s, the roots of biolinguistics are to be found in Chomsky's 1959 review of Skinner's book *Verbal Behavior*, which effectively put an end to the dominance of the behaviorist paradigm in psychology, and Lenneberg's comprehensive collection of evidence in favor of a biological substrate for the uniquely human capacity for language acquisition, which culminated in his classic 1967 book, "*Biological foundations of language*".

The significant change caused by Chomsky's review was to reorient scientific studies of language towards more internalist issues, revolving around the cognitive capacity that human beings bring to the task of language acquisition, interpretation, and production—what Chomsky (1965) dubbed "linguistic competence". Chomsky went on to formulate a set of central, field-defining questions, all of which led logically to the realm of biology, converging with the range of evidence revealed by Lenneberg (critical period, creolization, language impairments, etc.) This was in fact to be expected, as both Lenneberg and Chomsky took as their point of departure the classic ethology literature (Konrad Lorenz, Niko Tinbergen, Karl von Frisch, and others), where (animal) behavior was studied "biologically".

The success of what is often called the "cognitive revolution" naturally led to the organization of interdisciplinary meetings, where linguists, biologists, neuroscientists, anthropologists, and experts in other disciplines such as Artificial Intelligence, convened to shed further light on the biological nature and evolution of the human language faculty. Historically speaking, the most prominent of these meetings was the "Chomsky-Piaget" encounter in Royaumont in 1975. It was, in fact, during a prequel of this encounter, in Massachusetts in 1974, that Massimo Piattelli-Palmarini (the mastermind

behind this and many subsequent meetings on biolinguistics; witness Piattelli-Palmarini, 1980; Piattelli-Palmarini *et al.*, 2009) came up with the term 'biolinguistics'. Interestingly for readers of this journal, in the transcript of the 1974 meeting to which I have had access, both the terms 'biolinguistics' and 'bioanthropology' were used interchangeably to refer to the same enterprise. It was indeed clear back then, as it is clear now, that, given the centrality of language for modern human cognition, a field focusing on the biological foundations of human language amounts to one intent on uncovering what one might call "the human mind's body plan", which I take to be the ultimate subject matter of bioanthropology. But while biological anthropology achieved independence from cultural anthropology and flourished, biolinguistics did not. Biological concerns remained confined to introductory sections of linguistics papers, and substantive engagement with the biology literature on the part of linguists remained scarce. This is in part because at the end of the 1970s theoretical linguistics developed successful models of cross-linguistic comparisons (Chomsky, 1981; Baker, 2001), and biological concerns were relegated to the background. It is only recently—about ten years ago—that the term 'biolinguistics' resurfaced, and with it, the interdisciplinary concerns that were at the heart of the cognitive revolution in the 1950s.

In this overview article I examine the factors that led to this biolinguistic revival, discuss the progress made since then, and highlight both prospects and challenges raised by recent studies. Towards the end of the article, I also formulate some personal suggestions intended to advance the field, incorporating important results from the anthropological sciences that linguists have perhaps not yet assimilated fully. (Readers wishing to learn more about the early history of the field succinctly addressed in this introduction section are encouraged to consult Jenkins, 2000; Boeckx, 2009a; Di Sciullo & Boeckx, 2011; Boeckx & Grohmann, 2013.)

I should stress that the field of biolinguistics is still in its infancy. Although its major goals are clear, like many similar interdisciplinary

enterprises, it suffers from the many differences that exist among perspectives, methodologies, and even discrepancies in terminology. Too many scholars still put forth rather naive hypotheses about language, ignoring the substantial progress regarding the computational nature of human language over the past 50 years—a progress unmatched in the context of cognition (with the possible exception of early vision). There is a serious need for linguists to make the essential aspects of this progress available, in an accessible form, to other fields. To achieve this, it is necessary for linguists to engage substantially with the biology literature, something which I recognize has not yet happened enough, hence the feeling among some biologists that little has been achieved in terms of concrete results in biolinguistics. The overall message of this review is that there are grounds for renewed optimism in this area.

Factors that led to the comeback

The return of 'biolinguistics' is due to a variety of factors, which I would like to first list and then elaborate on in this section. The factors are:

1) The progress made possible by the genomic revolution in genetics, which led to the discovery of *FOXP2*, insights into its evolutionary history, and its interactome (Lai *et al.*, 2001; Enard *et al.*, 2002; Konopka *et al.*, 2009) and which promises much more in the coming years;

2) The rise of a bottom-up perspective in comparative psychology, and its increased appreciation that the basic building blocks of cognition might be shared across a wide range of species, in line with Darwin's notion of descent-with-modification (De Waal & Ferrari, 2010; Hauser *et al.*, 2002), which opens up the possibility of constructing 'cognitive phylogenies' (Fitch *et al.*, 2010);

3) A reduction of the theoretical machinery needed to account for the fundamental properties of grammar within linguistics— a theoretical trend known as 'linguistic

minimalism' (Chomsky, 1995, 2007a; Boeckx, 2006, 2011d), which renders the study of the language faculty more feasible biologically speaking, both in terms of its emergence, as it minimizes the cognitive boundaries across species, and in terms of its neural implementation;

4) A decidedly pluralist agenda in biology: 'evo-devo' and its 'extended synthesis' (Pigliucci & Müller, 2010), which provides enough theoretical flexibility to handle a complex bio-cognitive object like the human language faculty.

Molecular windows

The logical deduction that the faculty of language is somehow part of our biological endowment cannot match the excitement of actually discovering genes more or less directly related to linguistic behavior. It is for this reason that the discovery of the link between a specific mutation of the *FOXP2* gene and a linguistic disorder (attested in the now well-known KE family) played a crucial role in revitalizing the study of the genetics of language. The point, of course, is not to look for 'language genes' or 'grammar genes', but to uncover the molecular basis of what ultimately makes typical language development possible. A healthy dose of skepticism towards geno-centrism notwithstanding, the genomic revolution makes available new tools and new pools of data whose relevance for biolinguistics cannot be overstated.

There are several excellent reviews of the steps that led to the discovery of the relevance of the *FOXP2* gene, and of the implications that the early results raise for the relationship between genetics and linguistics. I say 'early results' because scarcely a month goes by without new information about the gene and its interactome, but Marcus & Fisher (2003), Ramus (2006), Fisher & Scharff (2009), Piattelli-Palmarini & Uriagereka (2011), Berwick (2011), Scharff & Petri (2011) and Benítez-Burraco (2012, 2013) provide excellent overviews. Here I would like to focus on what I take to be some of the most important lessons learned so far. These will also

serve as illustrations of some of the conceptual barriers faced by biolinguists.

The first one is that in order to link genes ('bio-') and mind ('ling'), it is imperative to develop linking hypotheses involving the brain, for there is no direct road from genes to cognition. As Marcus (2004) aptly put it, "genes build neural structures, not behavior". In fairness, even this statement is too simplistic, as genes do nothing on their own. To get to neural structures, epigenetic processes must be taken into account. But Marcus's assertion certainly goes in the right direction, as it highlights the distance between genes and cognition. And there's the rub: linguists, and cognitive scientists more generally, still don't have a good understanding of how brain and mind relate to one another. In recent years, several important reflections have appeared concerning why this is so (Poeppel & Embick, 2005; Gallistel & King, 2009 are outstanding), to which I will come back in this article, but for now, let me make clear that until we fix this problem, we have little hope to interpret properly the information that comes out of genetics labs.

The second lesson to draw from inquiries into the role of *FOXP2* is that valuable as the information concerning the evolutionary of the gene is (as is well known, *FOXP2* is a highly conserved gene, with only two amino acids separating the human version from the chimp version, and only three amino acids separating the human version from the mouse version), it will be extremely hard to draw inferences from it concerning the evolution of the language faculty. For example, attempts have been made to establish recent selective sweeps (Enard *et al.*, 2002), but they remain extremely controversial, both concerning the timing of the sweep (Coop *et al.*, 2008) or the very nature of the sweep itself (Ptak *et al.*, 2009; Berwick, 2011; Benítez-Burraco *et al.*, 2008), due to inherent methodological reasons (the choice of initial conditions to detect the sweep; cf. Lewontin, 2002; Garrigan *et al.*, 2010), and also because it is hard to be sure about selective pressures given the many sites of *FOXP2* expressions beside the brain (lung, heart,

etc.) and the possibility of free-riding functional effects in the context of pleiotropy.

It's also been claimed that Neanderthals (and Denisovans) had "language" because their genomes contained the modern human version of the gene (Krause *et al.*, 2007; Reich *et al.*, 2010), but again linking genes and cognition without solid intermediary hypotheses involving the brain is at this point a risky and largely speculative endeavor, as Longa & Benítez-Burraco, 2012 convincingly demonstrate. In addition, no gene acts on its own, and recent studies (Meyer *et al.*, 2012; Maricic *et al.*, 2012) strongly suggest that the context of expression of *FOXP2* was rather distinct in our extinct cousins, given our current understanding of the *FOXP2* interactome in modern human (Konopka *et al.*, 2009, 2012; Vernes *et al.*, 2008, 2009).

None of these difficulties are specific to *FOXP2* (in fact, as Piattelli-Palmarini & Uriagereka, 2011 rightly emphasize, some aspects of the *FOXP2* gene comes close to what a geneticist would dream to find, so future candidate genes are likely to be even messier!), it's just that biology is a messy business, as Richard Lewontin never tires of writing (Lewontin, 1993, 2000). Although one may find aspects of Lewontin's skepticism extreme (see, e.g., Lewontin, 1998), and indeed hope that "fossil genes" will shed light where more traditional kinds of fossils are missing (Carroll, 2006), no one should expect the story to be linear, easy, or intuitive. Certainly, there is no clear lead in this domain at the moment.

I also don't want to give the impression that the value of everything we have learned about *FOXP2* is unclear. Apart from having made it obvious that the link between *FOXP2* (genotype) and language (phenotype) is very indirect, solid progress has been made in at least three areas. First, it has provided a significant boost to cross-species comparison, and helped shed light on the neurobiology of vocal learning. Second, it has highlighted the relevance of subcortical neural structures in understanding the neural basis of language. Third, it has opened up the possibility of intra-species genetic variation in the normal population, which until

very recently was discarded, given the uniformity of language development.

Let me elaborate on each of these points, beginning with the last one. In the course of unravelling neurogenetic networks implicated in developmental language disorders, we have learned that certain genes regulated by *FOXP2*, such as *CNTNAP2*, are polymorphic, even in the normal population. Some of these variants have been shown to affect early language development in the general population (Whitehouse *et al.*, 2011), and to also underlie differences detected by various psycholinguistic measures in adults (Kos *et al.*, 2012). Studies of this kind (see also Pinel *et al.*, 2012 directly implicating *FOXP2*) cast doubt on the longstanding assumption that the "linguistic genotype" is going to be uniform across the species in the absence of a fairly severe and specific pathology. Indeed, they suggest that a continuum may exist between these pathologies and normal interindividual variability (an idea Antonio Benítez-Burraco and I are currently exploring) and that there may be more than one "normal" neurological organization for language (Hancock & Bever, 2013).

The discovery of the linguistic relevance of *FOXP2* also led to a renewed appreciation for the role of subcortical structures such as the basal ganglia, the thalamus, and the cerebellum in language (and cognition more generally). It is fair to say that neurolinguistics is still on the whole rather corticocentric, but tracing the neural expression of *FOXP2* during embryological development, and tracking the effects of *FOXP2* mutations on brain structure and function has contributed to reverting this trend (see Vargha-Khadem *et al.*, 2005), and lent credence to models that attribute a key role to subcortical structures (e.g., Lieberman, 2006). Recent knock-in experiments in mice reinforce this conclusion, as significant structural changes are observed in cortico-thalamo-basal ganglia circuits in mice carrying the humanized version of *FOXP2* (Reimers-Kipping *et al.*, 2011; Enard *et al.*, 2009); leading to the conclusion that *FOXP2* has contributed to tuning cortico-basal ganglia circuits (Enard, 2011). Other knock-in experiments in mice

(Fujita *et al.*, 2008; Fujita & Sugihara, 2012; Fujita *et al.*, 2012) have shown *FOXP2* targets such as *CNTNAP2* to exhibit distinct expression patterns in the cerebellum, another brain structure that is often missing from standard neurolinguistic models, despite its undeniable relevance (Murdoch, 2010; Barton, 2012; Deniz Can *et al.*, 2013; Saldaña Gascon, 2012).

To be clear, the cortex remains relevant. As a matter of fact, Tsui *et al.* (2013) conclude from new experiments in mice that *FOXP2* regulates genesis of some intermediate progenitors and neurons in the mammalian cortex, and suggest that the evolution of the gene may be associated with the expansion of the human cortex. But the relevance of cortico-thalamo-cerebello-basal ganglia loops for some aspects of language should now be clearer than ever. The big question, of course, is, which aspects of language? The brain structures just mentioned may give us a clue. In a recent review, Jürgens (2009) proposed two separate pathways involved in the control of vocalizations. The first runs from the anterior cingulate cortex via the midbrain periaqueductal gray into the reticular formation of pons and medulla oblongata and from there to the phonatory motoneurons. The second vocalization control pathway described by Jürgens runs from the motor cortex via the reticular formation to the phonatory motoneurons. This pathway has been shown to include two feedback loops, one involving the basal ganglia and the other involving the cerebellum. A comparison of vocalization pathways among terrestrial mammal species has revealed that only humans exhibit a direct pathway from the motor cortex to the motoneurons controlling the larynx muscles. In contrast, connections between the limbic cortex and the motoneurons constitute an ancestral trait found in many non-human species.

From this we could conclude that *FOXP2* acts on structures involved in the externalization of language, morpho-phonological processing, and the mapping from hierarchical to linear structures (see Kurt *et al.*, 2012 for relevant material). Interestingly, this is the area of language where cross-linguistic variation and the need for rule learning is most obviously attested (Boeckx, 2011a; Berwick & Chomsky, 2011).

Cortico-basal ganglia circuits, including their dopaminergic modulations, are also crucial for song learning in birds (Jarvis, 2006), and this brings me to the third positive effect of *FOXP2* studies in biolinguistics: the parallels between human language and bird song. Darwin (1871) had already recognized the relevance to language evolution of birdsong, which he considered the "nearest analogy to language". Like humans, many birds have fully instinctive calls, and an instinct to sing. But the songs themselves are learned. Darwin recognized the parallel between infant babbling and songbird "subsong", and recognized the key fact that cultural transmission ensures the formation of regional dialects in both birdsong and speech. Finally, he recognizes that physiology is not enough for learned song: crows have a syrinx as complex as a nightingale's but use it only in unmusical croaking. All of these parallels have been amply confirmed, and further explored, by modern researchers (Doupe & Kuhl, 1999; Marler, 1970; Nottebohm, 1970), but it was not until the *FOXP2* discovery that such parallels were exploited by biolinguists (see Bolhuis *et al.*, 2010). Today, this is one of the most productive areas of research in biolinguistics, as song birds offer a model organism for vocal learning (the only one, so far, but see Arriaga *et al.*, 2012 for the claim that mice also possess the basic neuroanatomy for vocal learning, opening up the possibility of a neurobiological continuum in this behavioral domain, as mooted in Arriaga & Jarvis, 2013). In addition, the structural variety of bird songs offers the beginning of genuine formal comparison with human language (Berwick *et al.*, 2011, 2012).

Looking back at what *FOXP2* has taught us so far (no doubt, but a fraction of what it will teach us in the future), I am tempted to say that this gene made it plain to us that the distance from genes to mind cannot be underestimated, but it also helped made us aware that something like "comparative biolinguistics" (focused on the inter- and intra-species variation that lies well beneath the surface variation that is the bread

and butter of comparative linguistics—the comparison of languages) may be in the making.

Innovation and specificity

Perhaps no paper symbolizes the return of biolinguistics as well as Hauser, Chomsky, and Fitch (2002). The paper is famous for introducing the Faculty of Language in the Broad [FLB]/ Narrow [FLN] sense distinction, and notorious for suggesting that the content of FLN is "recursion". In an attempt to reconcile what makes the language faculty unique (human specific) and properly Darwinian descent-with-modification scenarios (a program aimed "at uncovering both shared (homologous or analogous) and unique components of the faculty of language"), Hauser, Chomsky & Fitch (2002) distinguished between FLB and FLN, with the latter being defined essentially as what makes language human-specific. As Fitch, Hauser & Chomsky (2005) characterize it, "[i]t seems likely that some subset of the mechanisms of FLB is both unique to humans, and to language itself. We dub this subset of mechanisms the faculty of language in the narrow sense (FLN)."

Hauser, Chomsky and Fitch went on to implicate "recursion" in trying to add content to FLN. I use words like 'implicate' and put 'recursion' in quotes for, as readers of Hauser, Chomsky & Fitch (2002) will immediately notice, the exact position defended in the paper is not clear. Consider the following passages, all taken from the same paper:

1) "We hypothesize that FLN only includes recursion and is the only uniquely human component of the faculty of language" (p.1569, abstract)
2) "We assume ... that a key component of FLN is a computational system that generates internal representations and maps them into the sensory-motor interface by the phonological system, and into the conceptual-intentional interface by the (formal) semantic system. ... All approaches agree that the core property of FLN is recursion" (p.1571, column 1)

3) "In fact, we propose in this hypothesis that FLN comprises only the core computational mechanisms of recursion as they appear in narrow syntax and the mappings to the interfaces" (p.1573, column 2-3)
4) "At minimum, then, FLN includes the capacity of recursion" (p.1571, column 3)

Unfortunately, this infelicity attracted most of the attention in the subsequent literature. This, in my opinion, was doomed to be unproductive because "the core computational mechanisms of recursion as they appear in narrow syntax and the mappings to the interfaces" alluded to by Hauser, Chomsky and Fitch were never explicitly stated in that paper (nor in the 2005 sequel), making the claim about "recursion" too vague to be falsified. Because of this focus on "recursion", most of the literature has tried to determine "what is in FLN", but I think that this was the wrong strategy: the emphasis should have been on FLB, for the recognition that a significant amount of the language faculty could be neither specific to language nor unique to humans marked a rather sharp departure from the standard position in the dominant biolinguistic paradigm in its early days. As Chomsky (2007a) has observed, "[t]hroughout the modern history of generative grammar, the problem of determining the character of [the] F[aculty of] L[anguage] has been approached "from top down": How much must be attributed to U[niversal] G[rammar] to account for language acquisition? The M[inimalist] P[rogram] seeks to approach the problem "from bottom up": How little can be attributed to UG while still accounting for the variety of I-languages attained?" This significant shift of perspective in linguistics is, in fact, part of a sea-change within the cognitive sciences that makes what I have called "comparative biolinguistics" possible. This is well-captured in the following passage from De Waal & Ferrari (2010):

"*Over the last few decades, comparative cognitive research has focused on the pinnacles of mental evolution, asking all-or-nothing questions such as which animals (if any) possess*

a theory of mind, culture, linguistic abilities, future planning, and so on. Research programs adopting this top-down perspective have often pitted one taxon against another, resulting in sharp dividing lines. Insight into the underlying mechanisms has lagged behind ...

A dramatic change in focus now seems to be under way, however, with increased appreciation that the basic building blocks of cognition might be shared across a wide range of species. We argue that this bottom-up perspective, which focuses on the constituent capacities underlying larger cognitive phenomena, is more in line with both neuroscience and evolutionary biology".

Put succinctly, the more we attribute to FLB, the more biologically feasible FL becomes.

Having said this, I should hasten to add that the whole FLB/FLN distinction may not have been the most felicitous way of redirecting attention to the need for a comparative, as opposed to a contrastive, biolinguistics. Although Hauser, Chomsky, and Fitch wrote that "[l]inguists and biologists, along with researchers in the relevant branches of psychology and anthropology, can move beyond unproductive theoretical debate to a more collaborative, empirically focused and comparative research program" by adopting the FLN/FLB distinction ("The FLB/FLN distinction is critical for productive discussion of language evolution", according to Fitch, Hauser, and Chomsky (2005)), I find the very B/N dichotomy dubious, for reasons that deserve to be elaborated on.

Hauser, Chomsky & Fitch are certainly right in saying that "[s]omething about the faculty of language must be unique in order to explain the differences between humans and the other animals", but as Jackendoff & Pinker (2005) correctly point out, "the Narrow/Broad dichotomy [...] makes space only for completely novel capacities and for capacities taken intact from nonlinguistic and nonhuman capacities, omitting capacities that may have been substantially modified in the course of human evolution". Indeed, there are capacities that may have been substantially modified in the course of human

evolution to be included in FLB or in FLN. Take *FOXP2*. While highly conserved, the gene has undergone two mutations in our lineage. Say, for the sake of the argument, that we succeed in establishing that these mutations led to specifically (and uniquely) linguistic changes. Would the role of *FOXP2* be a component of FLB, or of FLN? FLN, it seems to me, but not according to Fitch, Hauser, and Chomsky (2005), who take the highly conserved nature of the gene to automatically make it part of FLB.

At the heart of the FLN/FLB distinction is the attempt on the part of Hauser, Chomsky & Fitch (2002) to grapple with the problem of innovation and novelty in biology. This problem is currently attracting a lot of attention in the "evo-devo" literature, after having been badly neglected in the context of the modern synthesis (as Mayr, 1960 readily acknowledged.) As is well known, while biologists have made great progress over the past century and a half in understanding how existing traits diversify, relatively little progress has been made in understanding how novel traits come into being in the first place. To remedy this explanatory deficit, Evo-Devo practitioners have first attempted to define what counts as a novelty (here the work of Gerd Müller has been especially illuminating; see especially Müller (2010) and Müller & Newman 2005). In this context, it is worth noting the similarity between how Fitch, Hauser & Chomsky (2005) define FLN ("that which is specific to language and unique to humans") with the definition put forth in Müller & Wagner, 1991: "*a structure that is neither homologous to any structure in the ancestral species nor homologous to any other structure of the same organism*".

Say that FLN counts as such a novel structure (I think this is the unstated intention of Hauser, Chomsky, and Fitch (2002)). If one turns to the relevant evo-devo literature, one finds a consensus regarding how such novel structures arise. The consensus position is what Müller (2010) characterizes as "Type II" or "emergent" novelty. For Müller, and for many other biologists that worry about such novelties (see Wagner & Müller, 2002; Moczek, 2008; Moczek & Rose,

2009; Prud'homme *et al.*, 2011; who provide several concrete examples of novelties), "phenotypic novelty is largely reorganizational rather than a product of, say, innovative genes" (West-Eberhard, 2003) (cf. the notion of "deep homology" in Shubin *et al.*, 2009, see also Balari & Lorenzo, 2013). In other words, novelty arises from the combination of generic mechanisms, whose collective effects give rise to what appears to be *de novo* characters (phase transitions).

Interestingly, the possibility of emergent novelty is alluded to in Fitch, Hauser, and Chomsky (2005, p.182): "*Something about the faculty of language must be unique in order to explain the differences between humans and the other animals if only the particular combination of mechanisms in FLB*". But they fail to note that this puts in jeopardy the very FLN/FLB distinction (with FLN taken to be a subset of FLB, as made clear in Hauser, Chomsky & Fitch 2002). Incidentally, the possibility of emergent novelty is present in some of Chomsky's own works (Chomsky, 1980, 2000), but is always put in doubt ("*Now a question that could be asked is whether whatever is innate about language is specific to the language faculty or whether it is just some combination of the other aspects of the mind. That is an empirical question and there is no reason to be dogmatic about it; you look and you see. What we seem to find is that it is specific.*"). This is unfortunate, for Chomsky's stance (which boils down to the FLN/FLB distinction) indeed "mak[es] some hypotheses — in our view the most plausible ones — impossible to state" (Jackendoff & Pinker, 2005). Not surprisingly, one finds the following statement in Fitch's recent writings (in direct contradiction from the affirmation in Fitch, Hauser & Chomsky (2005) and already quoted above that the FLN/FLB distinction is "critical for productive discussion of language evolution"):

"*What all of these examples make clear is that the distinction between general and linguistically specialized mechanisms is hard to draw, even in those cases where the mechanisms themselves seem fairly clearly defined. Most areas of language are not, and will not soon be, so*

clearly defined, and thus the distinction itself is of little use in furthering our understanding of the mechanisms". (Fitch, 2011, p.384)

On the basis of this, I am led to conclude, with Bloomfield, Gentner, and Margoliash (2011), that "[p]erhaps this is a good time to reconsider whether attempting to distinguish between qualitative and quantitative differences is helpful if the quantitative advantage is vast." It is indeed puzzling that so many researchers still cling to the FLN/FLB distinction when the rationale behind the distinction given at the outset of Hauser, Chomsky, and Fitch (2002) is to reject the notion of the faculty of language as a monolithic object: how can we identify if some mechanism is 'specific to language' if 'language' itself is not a well-defined, unique object. Perhaps it is for this reason that the phrase "unique/specific to language" does not appear in the original 2002 paper (Joana Rosselló, pers. comm.), but only appear as such in Fitch, Hauser, and Chomsky (2005), who take it from Pinker & Jackendoff (2005), where FLN is characterized in those terms for the first time (contrary to the literature that routinely attributes it to Hauser, Chomsky & Fitch, 2002).

Grammatical downsizing

The most promising aspect of Hauser, Chomsky & Fitch (2002) is the idea that much of what linguists have attributed to the language faculty falls in the broad characterization of it; that is, many properties of the human language faculty are neither specific to language nor specific to humans. This conclusion converges with the 'minimalist' project that many formal linguists embarked on in the 1990s (see Chomsky, 1995; Boeckx, 2006, 2010, 2011d, among many others). Linguistic minimalism is an attempt to minimize the role of system-specific assumptions to account for properties of natural language grammars.

Over the years it has become clear that the success of this minimalist enterprise depends on several factors that mesh well with biolinguistic concerns. First, it must rely on—and therefore

assume the existence of—a rich cognitive apparatus with which the (minimal) specifically linguistic apparatus interfaces to yield the substantive universals that previous linguistic research had (somewhat blindly) attributed to a highly structured and specifically linguistic "Universal Grammar". (In other words, the success of the minimalist project depends on the success of comparative biolinguistics.)

The rich cognitive apparatus in question covers both systems of interpretation ('meaning') and of externalization ('sound/sign'). This has effectively led to a model of the language faculty where many semantic and phonological aspects of language find their roots in capacities independently attested in other species. For phonology, I recommend Yip (2006), Samuels (2011), Samuels *et al*. (in press); for semantics, Hurford (2007) is outstanding, but the following are also excellent sources of information: Burge (2010), Carey (2009), Carruthers (2006), Hauser (2001), Cheney & Seyfarth (1990, 2007), Jackendoff (1990, 2010).

This is not to say, of course, that there is nothing specific about human language semantics or phonology. Rather, the emerging consensus is that specificity arises when ancient mechanisms are placed in a new context. In particular, the dominant view in minimalism ought to be that the emergence of a capacity to form potentially unbounded hierarchical structures of a particular sort, characteristic of human language (technically known as 'headed' or 'endocentric' phrases, i.e. groupings organized around a prominent element, such as a verb in a verb phrase) significantly reshaped the semantic and phonological components inherited by descent. Such a possibility is defended in Samuels (2011), Boeckx & Samuels (2009) for phonology and in Uriagereka (2008), Hinzen (2007, 2011), Pietroski (2011, to appear), Boeckx (2009b, to appear a) for semantics.

It is also becoming extremely clear that the success of the minimalist project will depend on recognizing that the emergence of many grammatical properties of natural languages is the product of social transmission and cultural evolution.

This effectively means that the success of this 'Chomskyan' enterprise depends on the correctness of approaches that have (erroneously, in my opinion) traditionally been put in opposition with 'Chomskyan' linguistics (e.g., Kirby, 2001; Kirby & Hurford, 2002; Kirby *et al*., 2008). As Boeckx *et al*. (in press) stress, building on Deacon's (2006) orders of emergence, such approaches—typically couched in terms of 'grammaticalization' and imperfect learning across generations—must be correct when it comes to accounting for the sort of cumulative complexity that characterizes morphophonological systems of specific languages (the systems of regularities and exceptions that lay people often take to exhaust what linguists mean by 'grammar'; "third-order emergence" in Deacon's typology).

The conclusion just reached is typically resisted in 'Chomskyan' circles, but it is, I think, inescapable. (If I am right, this illustrates how biolinguistics forces one to transcend the traditional 'ideological' boundaries that populate linguistic circles.) As Hall (2012) correctly observes, "pursu[ing] a biolinguistic approach to ... language, ... [i]n one sense means that the field of inquiry becomes broader." A successful biolinguist must know enough about the cognitive systems of other species and about the properties of non-linguistic cognitive domains in humans to be able to make reasonable inferences about what each of them contributes towards the shape of the modern language faculty. But "[i]n another sense, the central object of study becomes much smaller" for Chomskyan linguistics, for many of the grammatical details that were often attributed to some rich innate component specifically dedicated to language ('Universal Grammar') is to be understood in terms of cultural evolution. The empirical and explanatory success of approaches like Blevins (2004) reinforces this conclusion, and I anticipate that this trend will become more prominent in the field in years to come, especially in the context of cross-linguistic variation (Newmeyer, 2005; Boeckx, to appear b).

In a certain sense, the offloading of grammatical properties onto external factors converges with the claim advanced by Deacon (2010) that aspects

of language should be understood not as the result of selection pressures (that often lead to the internalization or genetic assimilation of certain traits), but in terms of relaxed selection. The net effect of relaxed selection is for speakers to have to rely on social transmission to reliably develop complex grammatical systems, and to possess a plastic, underspecified (i.e., minimally specified) 'innate' initial state of the language faculty ("Universal Grammar").

As I have discussed at length elsewhere (Boeckx, 2012b), the picture of the language faculty that emerges from minimalist guidelines rigorously pursued is one where the aspects of language geared towards externalization are much more complex and varied than those aspects dedicated to meaning. For the latter, the minimally specified structural properties of the language (what linguists often call 'narrow syntax') appear to be sufficient to exploit the rich conceptual resources inherited by descent to yield the range of rich interpretations that characterize human thought. Put succinctly, the contribution of the internal structural component of the language faculty is asymmetric; it appears to be better designed for meaning than for articulation (on this point, see also Berwick *et al.*, 2013).

As should be obvious, if something like what I have touched on in this section is on the right track, the modern human language faculty is a mosaic, with old, inherited parts put together in a new context (which boils down to the presence of a mechanism for generating unbounded hierarchical expressions), and further modified (complexified) by external influences (the external context of cultural, imperfect transmission). (On the non-uniform character of the language faculty, see also Heinz & Idsardi, 2013). It turns out, then, that debates about saltation vs. gradualism surrounding the language faculty as a whole, though extremely common (see Pinker & Bloom, 1990; Jackendoff, 2002) are misplaced and misleading (see also Clark, 2013), for the modern language faculty is not a uniform, monolithic object: some parts have fairly direct homologs while other parts are likely the result of abrupt phase transitions.

Evolutionary pluralism

In its 60 years of history the biolinguistic program has developed under the influence or inspiration of several biological paradigms. For instance, the role of ethology in the early days of biolinguistics has been well-documented (Chomsky, 1972; Boeckx, 2009a). Later on, in the course of the first biolinguistic meetings of the 1970s, Chomsky familiarized himself with the work of François Jacob and Jacques Monod on genetic regulation (Jacob & Monod, 1961), which provided the conceptual model for his parametric approach to cross-linguistic variation (as acknowledged in Chomsky, 1981, 2007b, 2009). More recently, several biolinguists have acknowledged the role of recent developments in evolutionary-developmental biology ("EvoDevo") in their writings (Balari & Lorenzo, 2013; Chomsky, 2010; Hauser, 2009a).

The rise of Evo-Devo is, indeed, an important factor in the characterization of the revival of biolinguistics, for the field of Evo-Devo offers a new space of conceptual options to understand the origin, evolution, and development of the language faculty that is at once broader than, and more congenial to long-standing themes in (bio)linguistics, than the neo-darwinian modern synthesis (see Boeckx, 2011c) on this point; remember also the discussion above concerning evolutionary novelties, and also concerning the relevance of fossil, highly-conserved genes). With its emphasis on gradualism and selectionism, the latter was the perfect incubator for evolutionary psychology (see, e.g., Pinker & Bloom, 1990). But the difficulties of strict, or exclusively selectionist approaches to language evolution (Piattelli-Palmarini, 1989; Uriagereka, 1998) made it look like linguistic investigations were out of tune with mainstream biology. At times, this led to non-sensical claims that "Chomsky" had to be "reconciled" with "Darwin"—claims that can only be made if the richness of Darwin's (and Chomsky's) writings is ignored.

Not surprisingly, when a more extended synthesis is pursued in biology (see Pigliucci & Müller, 2010), it becomes much easier to relate biolinguistic proposals to the biology literature.

As a matter of fact, several authors have pointed out that Lenneberg's research program was very much evo-devo *avant la lettre* (Boeckx & Longa, 2011; Balari, 2012); indeed, Lenneberg's writings display an awareness of the need to adopt a pluralist attitude towards the complex nature of the language faculty that is more in line with evo-devo calls in favor of an extended synthesis in biology than recent biolinguists' appeal to evo-devo, since these retain a more limited, molecular understanding of evo-devo (Benítez-Burraco & Longa, 2010, on this point; see also Müller (2008) on why molecular evo-devo, of the sort popularized by Carroll (2005), is not the most distinctive feature of the evo-devo paradigm).

This is all to say that a complete assimilation of everything that evo-devo has to offer to biolinguistics is still very much a task for the future, but one that promises a lot, not only in the context of language evolution studies (and the evo-devo emphasis of the centrality of the problem of phenotypic innovations, already discussed in the previous subsection in the context of Hauser, Chomsky, and Fitch, 2002), but also in the context of language development (Longa & Lorenzo, 2008, 2009, 2012), and in the context of what I have called comparative biolinguistics. If it is indeed the case that we find intraspecies variation involving genes that have a role to play in language, it is necessary to adopt a less geno-centric, and more epigenetic/dynamic perspective (of the sort evo-devo favors) to have any hope to account for why, despite genetic variation, language development is uniform across the species (barring severe pathology).

Emerging trends

To conclude this section, I'd like to mention two additional important considerations animating current biolinguistic research. Although these two factors have not led to the revival of the field, unlike those discussed so far in this section, they are poised for dominance in years to come, given the frequency with which they figure in recent papers.

The first of these two factors is the role the "Chomsky hierarchy" is to play in assessing the linguistic capacities of other species. In the wake of Hauser, Chomsky & Fitch, (2002) and the shift of emphasis in comparative psychology, Fitch & Hauser (2004) sought to assess the cognitive capacities of cotton-top tamarins by (and compare them to humans), using as a scale the formal language hierarchy (commonly known as the "Chomsky hierarchy"). Building on Chomsky's (1956, 1957) foundational results concerning the limitation of finite-state machines to capture natural language generalizations, Fitch & Hauser (2004) claimed that cotton-top tamarins, unlike humans, could not detect structures in stimuli that went beyond the computational capacity of finite-state automata. The results proved controversial in more than one way, but so have the results suggesting that some songbirds performed beyond the finite-state boundaries (Gentner *et al.*, 2006; Abe & Watanabe, 2011). (For review, see Berwick *et al.*, 2012, and also Van Heijningen *et al.*, 2009.)

The overarching problem, it seems to me, is the adequacy of the Chomsky hierarchy in assessing cognitive profiles. Although formal language theory can certainly help in designing experiments shedding light on mental abilities (see the papers collected in Fitch & Friederici, 2012), it suffers from a major problem in the context of biolinguistics. As is well-known, the Chomsky hierarchy is of limited use in characterizing human linguistic competence. As Berwick *et al.* (2012) correctly observe, the hierarchy is both "too weak and too strong", failing as it does to cut natural language at its joints (see also Heinz & Idsardi, 2011; Boeckx & Uriagereka, 2011).

Finding a substitute to the Chomsky hierarchy to construct cognitive phylogenies will be a serious challenge for the years to come. It is a challenge that ought to be of interest to anthropologists as well, given recent attempts to use the Chomsky hierarchies to draw cognitive inferences from artifacts in the fossil record (Camps & Uriagereka, 2006; Balari *et al.*, 2011; and Lobina, 2012; Balari *et al.*, 2012; Lobina & Brenchley, 2012 for an intense debate on the feasibility of this approach).

The second topic I want to touch on in this subsection pertains to how productive linking hypotheses between theoretical linguistics and neuroscience could be formulated. As I indicated above, this is a necessary step towards linking mind and genes, but also mind and the range of anatomical evidence drawn from the fossil records (e.g., skull size and shape). David Poeppel has written eloquently and accessibly about the challenges neurolinguistics faces (Poeppel & Embick (2005), Poeppel (2005, 2011, 2012). The heart of the matter, according to Poeppel, is the "granularity mismatch" (or "mapping") problem: the objects of study in theoretical linguistics and in neuroscience don't match. As a result, mapping one onto the other has proven impossible. Accordingly, Marr's (1982) vision of cognitive neuroscience based on linking levels of analyses, to which biolinguistics should aspire, remains distant.

Both theoretical linguistics and the neurosciences are to blame for this sorry state of affairs. For all the "bio" talk in linguistic circles, linguists have so far failed to distill what is known from linguistic theory into a set of computational primitives, and try to link these with models and specific principles of neural computation. As Poeppel points out, "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)." Put another way, "[l]inguists and psycholinguists owe a decomposition (or fractionation) of the particular linguistic domain in question (e.g. syntax) into formal operations that are, ideally, elemental and generic. ... Generic formal operations at this level of abstraction can form the basis for more complex linguistic representation and computation."

On the neuroscience side, the problem has been the emphasis on localization and spatial characterization of function. But localization is not explanation (this is Poeppel's "map" problem). What is needed instead is a set of mechanistic hypotheses to which findings in linguistic theory (or cognitive science more generally) could relate. This is, in some respect, the same concern voiced by Gallistel & King (2009), who point out that neurosciences (and, I might add, many fields of cognitive science) ought to take the notion of "computation" far more seriously than they have done so far.

Finally, both Deacon (2005) and I (Boeckx, 2012a, to appear a) have suggested, coming from different perspectives, that the failure to develop fruitful linking hypotheses in neurolinguistics may be the result on the part of linguists of having pursued an exclusively 'engineering' or 'lexicocentric' logic regarding how language works, as opposed to an 'embryonic' or 'syntactocentric' logic. The main difference between the two logics is that the former starts with small units of computation (say, words) and from there construct whole structures (say, phrases or sentences), whereas the latter takes the small units of computation to be the end products of a differentiation process starting from a much more generic, and underspecified whole. The main drawback of the engineering/lexicocentric perspective is that it invariably leads to starting assumptions that are so field-specific (e.g., the features of words in linguistics) as to be untranslatable (hence, useless) for researchers in other fields. As a result, all the generalizations based on these starting assumptions are lost in translation. A change in perspective (along the lines of how development is construed in embryology)—indeed, an inversion of reasoning—may prove far more productive.

A recent example of the rampant lexicocentric fallacy I have in mind (one which will be accessible to many readers, as it figures in an article targeting a wide audience) is to be found in the treatment of the differences between birdsong and human language offered by Berwick *et al.* (2012). (The lexicocentric stance is even made clearer in a follow-up paper: Miyagawa *et al.*, 2013).

Berwick *et al.*'s discussion bears on the influence of the lexicon because they take as

their point of departure famed ethologist Peter Marler's well-known contrast between "phonological syntax" and "lexical syntax" (Marler, 1970). On Marler's account, songbirds exhibit only phonological syntax, that is, the stringing together of elements, sounds, according to some well-defined pattern, but without the meaning of the resulting sequence as a whole dependent on the meaning of its individual parts. In contrast, Marler argues that only human languages exhibit lexical syntax, that is, changes in meaning resulting from different combinations elements such as word parts, words, or phrases. Put another way, Marler notes that while both birdsong and human language are combinatorial, in the sense that they both assemble larger structures out of more basic parts, only human language is compositional, in the sense that the meaning of a word or sentence changes as we change its component parts. Marler's use of the term "lexical syntax" may cause one to think that the key difference lies in the existence of lexical items ("words"). And indeed Marler's view leads to lexicocentrism, even if Berwick *et al.* (2012) appear to claim the contrary.

Thus, Berwick *et al.* (2012) note that "Marler's notion that it is "lexicoding" —words— that completely characterizes the division between human language and birdsong captures part, but not all, of the necessary distinctions." In particular, "[i]t does not account for the inherent asymmetry of human language structure, and falls short when it comes to describing human language structures that have no associated lexical meanings, such as the metrical or prosodic structure associated with human language." Elsewhere, they write, "we should emphasize that it would be a mistake to conclude that all birdsong-human differences result simply from the lack of words in birdsong, ... For example, even though birds lack words, there is nothing that logically blocks birdsong syntax from relying on syllable groupings or other features that could themselves be labeled by properties of their constitutive parts".

Berwick and colleagues conclude that "it is not the lack of words alone that blocks the possibility

of more complex birdsong syntax. Rather, this gap is due to a fundamental deficiency in a very particular computational ability, namely, the lack of the combinatorial operation of the sort found in human language [what is often called "Merge" in the theoretical linguistics literature—CB]".

However, Berwick *et al.* end up partially agreeing with Marler (and many others, e.g., Pinker & Jackendoff, 2005), because the notion of combinatorial operation/Merge they advocate is not the mere act of combining, but a lexicocentric version of it, as the following passage makes clear.

> "The key difference is the use of a verb or nouns features to label an entire word sequence with a single label, ... the selection of a privileged element in this way renders the underlying structure fundamentally asymmetric. Note that there is no analog to this in birdsong ... . Consider as an example the birdsong motif described earlier, consisting of seven particular syllables. This motif is not labeled by selecting just one of these syllables and its properties to name the entire motif; none of the syllables takes priority ... Neither is the resulting structure asymmetric as it is in human language. This is true precisely because birds apparently do not have words or manipulate word features at all. This is one difference between the human language syntactic system and birdsong. We noted earlier that this does not in principle bar the possibility of birdsong making use of features of song elements, for example, syllables and their acoustic features, and assembling them in a similar hierarchical fashion. However, current evidence suggests that this does not occur in birdsong. Rather, the combinatorial operator itself is absent".

By stressing the notion "labeling dependent on word features", Berwick *et al.* effectively end up "anchor[ing]" the combinatorial operator "on words or more precisely, word features", and conclude that

> "It is this operation [lexicocentric Merge— CB] that is apparently absent in birds, so

far as we know. However, even though birds seemingly lack words, it does not follow that the combinatorial operator is necessarily absent in birds. For example, the combinatorial operator could still work on other elements, for example, syllables, in this way yielding the distinctive metrical patterning of sound melodies, rhythmic patterns, … . However, for whatever reason, the operator does not appear to have been exploited this way in birds. It remains an open question as to whether a similar analysis would apply to birdsong metrical patterns; this then is a possibly crucial open research question where a non-human model might (speculatively) provide insight into its counterpart in human language. If birdsong were found to operate in a similar way to human metrical structure, this might provide precisely the required evolutionary "bridge," in the sense that the combinatorial operator was present in the common ancestor of both species, but full-fledged language required in addition words and their features, an ability present in the human lineage, but not in any bird species. It follows that it is precisely here that one might look for key evolutionary innovations that distinguish humans from birds …".

As I will discuss in the next section, my own view (defended in Boeckx, 2011b, c, to appear a) is quite different. For me, it's not the projection of (word) features, but the presence of an unrestricted combinatorial operator (corresponding to the notion of 'unrestricted Merge') that was the big evolutionary breakthrough. It was the possibility of ignoring word/conceptual features that made it possible for humans to make infinite use of finite means, and construct "finite-yet-unbounded" systems (in the sense of systems yielding endlessly many complex expressions that can be characterized recursively), which encompass language, mathematics, and music. Rather than seeing the evolutionary breakthrough as a constraint on merge (asymmetric labeling), we should think of it as the lifting of a constraint—the removal of selectional restrictions that block systematic combination of the sort we find in language (and in other domains

of human thought/activity, where words are far less central; think of music and mathematics).

Where to go from here: some personal suggestions

As I have stressed on several occasions in this review, a productive biolinguistics must be brain-based. It seems to me that much work in this area remains bound to ideas ultimately going back to Paul Broca, ideas that are in serious need of reconsideration. I am not here referring just to the classical model of language areas (with Broca's area and Wernicke's area occupying pride of place) —a model that numerous studies have shown to be hopelessly simplistic (see Hickok & Poeppel, 2007, to cite but one study), I am also referring to the idea, often attributed to Broca, that the defining characteristic of the human brain is its asymmetric character.

Timothy J. Crow is perhaps the most prominent advocate of the importance of brain asymmetry in the emergence of language and our species. Crow (2008, p.43) has indeed written that "If the innovation that allowed the evolution of language was genetic [...] lateralization of function in the brain (Broca's hypothesis) is the only current candidate mechanism." What Crow refers to as "Broca's hypothesis" is rooted in the following passage from Broca's writings (from Harrington, 1987, pp.65-66):

"Man is, of all the animals, the one whose brain in the normal state is the most asymmetrical. He is also the one who possesses most acquired faculties. Among these faculties-which experience and education developed in his ancestors and of which heredity hands him the instrument but which he does not succeed in exercising until after a long and difficult education-the faculty of articulate language holds pride of place. It is this that distinguishes us the most clearly from the animal".

But I think that a close reading of this passage, and of Broca's other writings, reveals a

somewhat different (and ultimately, I believe, more accurate) picture. Note that in the passage just quoted, Broca talks about "the faculty of articulate language". This is, by no means, an innocent phrase. Elsewhere, Broca (1861, p.334) writes (about aphasia)

"What is missing in these patients is only the faculty to articulate the words; they hear and understand all that is said to them, they have all their intelligence and they emit easily vocal sounds. What is lost is therefore not the faculty of language, is not the memory of the words nor is it the action of nerves and muscles of phonation and articulation, but something else ... the faculty to coordinate the movements which belong to the articulate language, or simpler, it is the faculty of articulate language".

In others words, Broca is distinguishing between the faculty of language and the faculty of articulate language. I believe that the distinction is important, and in fact relates to the asymmetric contribution of the internal structural component of the language faculty (the idea, already discussed above, that language appears to be better designed for meaning than for articulation, and quite possibly more robust to deviations and deficits in the former domain than in the latter). Broca may well be right about brain asymmetry being related to 'articulation' (externalization of linguistic expressions). After all, brain asymmetries are also found in other vocal learners, where semantics is missing (see Moorman et al. (2012) on lateralization is birds). And it would make a lot of sense to tie the externalizing, referential, communicative component of language and sexual selection via brain asymmetry (Crow's hypothesis concerning the human torque), if sexual selection is to be understood in terms of mate recognition mechanisms, which must then refer to overt behavior (and communication surely is one).

Brain asymmetry, then, following Broca, would be a tell-tale structural sign of the "communicative brain", as William Marslen-Wilson has called it. The communicative brain would be supported genetically by *FOXP2* and its interactome, which provide the basis for externalization systems (see Matsunaga *et al.* (2013) for data pointing in this direction), and may well be sexually selected for via *ProtocadherinXY*, as Crow has argued in numerous publications. It may even be the case that we may find *FOXP2* differences when sexes are compared (see Bowers *et al.*, 2013 for potentially relevant data). But, crucially, lateralization would not be the key to what one might call the "interpretive brain", where language appears to play its most distinctive role. To understand the latter, we must, I think, turn away from lateralization, and focus on a perhaps so far neglected aspect of *H. sapiens*' brain in the context of language, an aspect that is perhaps even more characteristic of our species than the structural asymmetries that have been the focus of so many studies: globularity.

It is now well-established that modern humans show a species-specific "neomorphic hypertrophy of the parietal volumes, leading to a dorsal growth and ventral flexion (convolution) and consequent globularity of the whole structure" (Bruner, 2004), well reflected in the archeological record (Bruner *et al.*, 2003; Bruner, 2004, 2010; Lieberman, 2011). Significantly, globularity is a trait absent in Neanderthals. I say significantly because the brain size range of modern humans and Neanderthals overlap, which has led many researchers to assume that the cognitive capabilities of these two species were similar. But we know that among humans the internal organization of the brain is far more important for cognitive abilities than its absolute size is. In other words, shape (wiring topology) may be far more significant than size is. We also know that the brain's internal organization depends on the 'tempo and mode' of brain development. And, interestingly, the attained globularity appears to take shape at a particularly significant point in development.

As Gunz *et al.* (2010, 2012) have shown, based on detailed measurements of internal shape changes of the braincase during individual growth, there are differences in the patterns of brain development between humans and Neanderthals during what everyone believes is a

critical phase for cognitive development. Gunz *et al.* (2010, 2012) reveal that when we compare the skulls of a Neanderthal and a modern human newborn, the Neanderthal's face is already larger at the time of birth. However, most shape differences of the internal braincase develop after birth. Both Neanderthals and modern human neonates have elongated braincases at the time of birth, but only modern human endocasts change to a more globular shape in the first year of life. This strongly suggests that modern humans and Neanderthals reach large adult brain sizes via different developmental pathways. (Neubauer *et al.*, 2010 show that the developmental patterns of the brain were remarkably similar between chimpanzees and humans after the first year of life, but differed markedly directly after birth. Quite plausibly, this means that those aspects of development that are shared between modern humans, Neanderthals, and chimpanzees as conserved, with modern humans, but not Neanderthals, depart from this ancestral pattern of brain development in the first year of life.)

As Gunz *et al.* (2010, 2012) observe, given that the differences between modern humans and Neanderthals are most prominent in the period directly after birth, they likely have implications for the neuronal and synaptic organization of the developing brain. The development of cognitive abilities during individual growth is standardly linked to the maturation of the underlying wiring pattern of the brain; and we know that around the time of birth, the neural circuitry is sparse in humans. We also know from clinical studies that even subtle alterations in early brain development lead to changes in the neural wiring patterns that affect behavior and cognition. It is therefore plausible to claim, as Gunz *et al.* (2010, 2012) do, that the connections between diverse brain regions that are established during this period in modern humans are significant for cognition. That is to say, it is unlikely that Neanderthals had the same cognitive profile as *H. sapiens*.

Indeed, I suggest that the mechanisms giving rise to globularity provide the basis for the distinctive mode of thought displayed by our species, which I'd like to call cross-modular thinking.

Numerous comparative studies in psychology reveal that mature linguistic creatures transcend many cognitive limits seen in animals and prelinguistic infants (infants whose linguistic capacity has not matured yet). Such limits are the signature limits of what Elizabeth Spelke has called core knowledge systems, which correspond to primitive knowledge modules in roughly the sense of Fodor (1983). Such systems (for space, numbers, actions, objects, social interactions, and perhaps a few more) suffer from informational encapsulation and quickly reach combinatorial limits (see Spelke, 2003 for a survey; see also Carruthers, 2003, 2006; Pietroski, 2007). By contrast, linguistically mature individuals regularly go beyond the computational boundaries of core knowledge systems to yield markedly different modes of conceptualization. As Spelke stresses, such new modes of thought often correspond to what would result from the combination of otherwise encapsulated concepts; for example, the ability to think of sets of individuals plausibly results from the conjunction of thinking about sets and thinking about individuals in the same conceptual space. (Incidentally, this characterization matches that of cognitive fluidity in Mithen (1996), which is reflected in the archeological record, e.g., terianthropes.)

Spelke is, I think, right in taking language to provide the key combinatorics to make this possible. But it would be a mistake in my opinion to conclude from this that the key evolutionary event was a completely new mode of combination, given that the combination in question ("Merge") is as primitive as one can get: it boils down to set-formation. The key event, rather, must have been the ability to combine virtually any concept (from whatever (core) knowledge system) with any other concept (from the same or another knowledge system). That is, the key event was the lifting of a constraint. This alone gives us our unique cognitive profile, what Hauser (2009b, pp.192-193) has dubbed 'humaniqueness', which he characterizes in part as the ability to 'create and easily understand symbolic representations of computation and sensory input', to 'apply the same rule or solution

to one problem to a different and new situation', and to 'combine and recombine different types of information and knowledge in order to gain new understanding'.

Such a characterization of humaniqueness matches fairly well the characteristic of the 'neuronal workspace' model formulated in Dehaene *et al.* (1998) in the domain of consciousness (see also Tononi & Edelman, 1998). (It also matches the properties of the multiple-demand system of Duncan (2010), which relies on the same fronto-parietal regions, and those of the 'connective core' put forth in Shanahan, 2012.)

Inspired by Baars's (1993) Global Workspace model for consciousness, the 'neuronal workspace' model emphasizes the role of distributed neurons with long-distance connections, particularly dense in prefrontal, cingulate, and parietal regions, interconnecting multiple specialized processors and "broadcasting" signals at the brain scale in a spontaneous and sudden manner, forming a 'global neuronal workspace'. Through this workspace, Dehaene *et al.* claim that "modular processors can exchange information very flexibly", "information can be accumulated across time and across different processors", "incoming information arising from analog statistical inputs can be discretized", and "chains of operations and branching can be performed"— properties corresponding fairly to Hauser's characteristics of humaniqueness.

Already a century ago Ramon y Cajal had underlined the special morphology of the pyramidal cells from the cerebral cortex and suggested they might be the "substratum of the highest nervous activities". Building on this insight, Dehaene *et al.*'s view as key building blocks of the workspace "a distributed set of cortical neurons characterized by their ability to receive from and send back to homologous neurons in other cortical areas, horizontal projections through long-range excitatory axons." As they point out, "such long range corticocortical tangential connections include callosal connections and mostly originate from the pyramidal cells of layers 2 and 3", and propose that "the extent to which a given brain area contributes to the global workspace would

be simply related to the fraction of its pyramidal neurons contributing to layers 2 and 3, which is particularly elevated in dorsolateral prefrontal and inferior parietal cortical structures." These are particularly relevant regions in the context of globularity.

But in addition to these cortical regions, I believe we must take into account the thalamus. (As Dehaene *et al.* note, "the pyramidal neurons from layers 2 and 3 establish, in addition, vertical and reciprocal connections with layer 5 neurons and thus corresponding thalamic nuclei. These connections contribute to both the stability and the dynamics of workspace activity, via, for instance, self-sustained circuits, but also mediate the direct access to and from the processing networks.") Although the thalamus has been implicated in the context of many human-specific traits like intelligence or consciousness (see Crick, 1984; Steriade & Llinás, 1988; Min, 2010), its role in language (for which we have a much more robust theoretical characterization than for the two other traits just mentioned) has not been fully exploited (but see Crosson, in press; Hebb & Ojemann, in press).

Given its central location and well-established, pivotal relay function, it is likely that the thalamus found itself affected by this novel globular environment. Indeed, at the raw anatomical level, the thalamus acts as a necessary relay center to connect many brain structures that have already been implicated in research on language: the cortical areas with the basal ganglia and with the cerebellum. Second, the literature on *FOXP2* and its interactome has often mentioned the thalamus as an important expression site of the genes involved (Vargha-Khadem *et al.*, 2005; Reimers-Kipping *et al.*, 2011; Enard *et al.*, 2009; Enard, 2011). Third, despite the cortical focus of many imaging studies and the technical difficulties in getting recordings from the thalamus, this brain structures role has been highlighted in neurolinguistic studies (see, e.g., Wahl *et al.*, 2008; David *et al.*, 2011). Finally, outside of language proper, the thalamus has routinely been assigned a key role in controlling attention, regulating oscillations generated in the cortex, etc. (see Saalmann

et al., 2012, among many others) functions that, though not specific to language, must surely also be part of a comprehensive neural characterization of language.

For all these reasons, the 'triangle' formed by the fronto-parietal lobes and the thalamus (with the latter regulating the dynamics of the former, as a clock does, possibly along the lines of Buzsáki, 1991) are, I think, good focus candidates of future biolinguistic studies. (As my references to Dehaene *et al.* (1998) have made clear, the literature on consciousness will prove particularly useful. This would not have come as a surprise to Darwin, who wrote in (1871, p.126), "If it could be proved that certain high mental powers, such as the formation of general concepts, self-consciousness, etc., were absolutely peculiar to man, which seems extremely doubtful, it is not improbable that these qualities are merely the incidental results of other highly-advanced intellectual faculties; and these again mainly the result of the continued use of a perfect language." On the role of language in consciousness, see especially Jackendoff, 1987.)

If the above remarks are on the right track, at least four major consequences are worth pointing out. First, uncovering the molecular underpinnings of the species-specific globularization phase is likely to yield important insights into the genetic basis of language. This is a task I recently undertook with the help of Antonio Benítez-Burraco incorporating candidates that may not have been included if only speech disorders were taken as point of departure. In this context, it is worth pointing out that a comparison of Neanderthal and modern human genomes revealed several regions with strong evidence for positive selection within *Homo sapiens*. Three among these are likely to be critical for brain development, as they affect mental and cognitive development. But other genes are clearly involved in giving rise to globularity, such as *RUNX2*, which affects the morphology of the cranium.

Second, the brain model for language will be far more distributed, and less cortico-centric (in line with much recent work, see Fedorenko

et al., 2010), as it will include structures like the basal ganglia, the cerebellum, and the thalamus as the coordinator of this orchestra. This in turn will mean that traditional regions like Broca's will likely play a less central role, much more closely related to externalization (see Boeckx & Martínez-Álvarez, 2013 for a specific proposal implicating Broca's region in the action of linearization, a property that could be related to the motor processing of other hierarchical structures, such as the action grammar patterns discussed in Fujita, 2009).

Third, if cross-modular thinking is such an important feature of the human language capacity, linguists in particular will have to soften their stance concerning language and modularity (and specificity), and adopt positions such as the one advocated in Newport (2010) or Marcus (2006), which converge in interesting ways with that of Karmiloff-Smith (1992), and indeed, with many evo-devo studies on modularity; cf. Callebaut & Rasskin-Gutman (2005), Schlosser & Wagner (2004) - positions that take modularity and specificity to emerge as a matter of development, in the context of a logic of reciprocal causation of the sort emphasized by Lewontin (2000).

Fourth, the reflections in this section are, obviously enough, only part of the whole story. At best, the evolutionary steps leading to globularity and anatomically modern humans only led to cognitively modern humans (taking the mind (cognition) to be what the brain (anatomy) makes possible), which took place around 200KYA. But from there to behaviorally modern humans, there is still a long way, which I assume requires a fair amount of cultural evolution, and a deeper understanding than we currently have of the social and environmental factors that led to some of the most dramatic signs of modernity well over a hundred years after the emergence of our species (see Sterelny, 2011 for valuable remarks). The (social, cultural, demographic) factors leading to this niche construction are likely to have affected the surface properties of languages, and the ways in which language is put to use. But this is another story, distinct from the emergence of the human language faculty.

Conclusion

Back in (1975), Chomsky could write that "[w]e know very little about what happens when 10^{10} neurons are crammed into something the size of a basketball, with further conditions imposed by the specific manner in which the system developed over time." We are now in position to take advantage of progress in numerous disciplines to be able to say a bit more about this. Combining information from (paleo)genetics, paleoneurology, neuroscience, linguistics, comparative psychology, and evolutionary biology, reviewed in this article, offers the contours of a new neurobiological architecture supporting that most distinctive trait of our species, the human language faculty.

Acknowledgments

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