

What Lenneberg Got Right: A Homological Program for the Study of Language Evolution

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By 1967, it was clear to Eric Lenneberg that reconstructing the phylogenetic history of language should require the adoption of a non-functional (or Owenian) homology concept for grounding relevant comparisons. Fifty years later, most biolinguistic approaches have betrayed this project, for they routinely derive their conclusions regarding the unique/shared status of language on merely folk grounds—as dramatically illustrated in Hauser, Chomsky & Fitch vs. Pinker & Jackendoff's debate, or based on functional considerations—as in Chomsky's recent conceptualization of language as a unique tool for thought. Here we claim that Lenneberg's project needs to be resumed and we articulate some suggestions about how to conduct it, taking advantage of recent findings and new conceptual insights concerning two crucial levels of analysis actually pinpointed by him—namely, anatomical/molecular structure and physiological function.

Keywords: homology thinking; character concept; evolutionary novelties; computational mind

Homologies cannot be established by relying on similarity that rests on superficial inspection [...]; on logical rather than biological aspects [...]; and on anthropocentric imputation of motives.
—Eric Lenneberg (1969: 641)

1. Introduction

It takes an easy exercise of folk comparative biology to persuade a freshman of the uniqueness of language when compared to the closest nonhuman behaviors that could possibly come to mind—say, the songs of oscine birds, the alarm calls of vervet monkeys, etc. As far as one can say, none of these otherwise sophisticated capabilities appears to provide the means for establishing complex sound-meaning pairings—alternatively, gesture-meaning pairings, ranging across any imaginable experiential domain, and with an open-ended capacity for composing new complex expressions from a finite array of preexistent basic units. In other words, a relatively shallow awareness of some Hockett-style definitional properties of language

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(Hockett 1960), together with some familiarity with songs, calls, or other nonhuman ways of signaling, appear to suffice to strongly fix the persuasion that language is uniquely human. At its proper (folk) level of observational accuracy, the statement is innocuous—perhaps even true, in the sense that it is true that France is hexagonal at a certain level of observational accuracy, as famously stated by Austin (1962: 143). But at a deeper level, one already subject to the strictures of biology proper, the matter becomes empirical and one to which expedient answers should not be welcome. To put it plainly, whether language is or is not a uniquely human capacity is clearly a matter of scientific discovery, the fulfillment of which obviously asks for a collaborative effort of theoretical linguistics and comparative biology at different levels of organization—say, from molecules to behavior. Moreover, and crucially to the point to be made here, such an effort is pointless if not conducted under the overarching umbrella of ‘homology thinking’, in the sense recently put forward by the likes of Ereshefsky (2012) and G.P. Wagner (2015). It may strike outsiders as surprising that the upsurge of evolutionary linguistics in the last few decades has made its way alien to such a reasonable guideline.

But it should strike insiders likewise, for it was already clear to Eric Lenneberg, as soon as in 1967, that any serious statement concerning the phylogenetic status of language must rely on *bona fide* structural and functional comparisons—be it at the anatomical, physiological or molecular levels of analysis, and disregarding the kinds of design and teleological considerations on which folk statements are commonly based. It clearly is a historical mistake of today’s biolinguistic approach to language evolution to have sidestepped Lennenberg’s wise advice in paragraphs like the following:

A study of design features may give us insight into some of the biases that enter into the process of natural selection, into the biological usefulness of certain features of animal communication but it is not relevant to the reconstruction of phylogenetic history. For the latter we are only interested in the relation of types of anatomical structure (including molecular structure) and physiological function (including motor coordination and sensory acuity), but we disregard the *usefulness* or *efficiency* of these features to the contemporary form.

(Lenneberg 1967: 234, emphasis in original)

The issue of deciding whether language is a new, unique organ of the cognitive make-up of humans, or rather an old, more or less widely shared one also present in the cognitive constitution of other species, is clearly a concern for homology thinking, understood along the lines of Lenneberg’s suggestion.

Let us clarify before proceeding that it is not the case that deciding whether what humans do with language is unique or at least special is a matter devoid of any biological interest. It is, of course, a biologically interesting question, but in the context of ‘population thinking’—a complementary branch to homology thinking within evolutionary biology (G.P. Wagner 2015), interested in deciding which selective pressures, if any, could possibly have favored the stabilization of language in the primeval human populations. But note that regarding this question, whether language is or is not an organ—new or otherwise, is not particularly demanding. Let us also note that for other evolutionary concerns—namely, the ones related to

so-called 'tree thinking' (G.P. Wagner 2015), considering language as 'new' (strictly speaking, an 'autapomorphy') may be critical if one credits it a role in fixing the position of humans within their closest nonhuman relatives. But in that case a loose notion of 'organ' may be enough. Actually, the role of autapomorphy is routinely credited to the absence of organs, or to traits that do not qualify as *bona fide* organs. In as much as 'something' (or 'nothing') offers a clue of the relative kinship between members of a group of species, it qualifies as an autapomorphy (Müller & G.P. Wagner 1991).

Let's stress this from the outset. Our main aim in this paper—in conformity with the goals of 'homological thinking'—has mostly to do with the individuation of organs, i.e. (1) how their identities can be established, so as to (2) verify how their shared or unique character can possibly be settled. In doing this, issues extremely important to the concerns of 'population' and 'tree thinking'—like adaptive function, adaptive change, kinship degree, etc.—become of a secondary interest. Their omission in this paper is thus not due to their lack of intrinsic importance, but to their low explanatory profile regarding the issues to be dealt with.

In this paper, we want to work out the idea that if one's goal has to do with establishing whether the natural history of 'language as an organ' starts with humans or it rather has an older pedigree, then practicing homological thinking is inescapable. And not only this, it is also inescapable doing it along the lines suggested by Eric Lenneberg, which are but the lines solidly grounded—but largely marginalized—by Richard Owen in the mid 19th century. One should not understand this as if questions of uniqueness/novelty only make sense as associated to organs—of course, they don't. But as a matter of fact, the idea of 'language as an organ' (Anderson & Lightfoot 2002) has been a persistent one all through the generativist tradition—but maybe not for the right reasons, and it is one that we believe will gain more credit and support in the near future. Both questions will be presently dealt with. Central to our claims is that it makes a lot of sense to consider the unique/shared condition of language at this particular level of analysis, departing from the most common position which holds that it only makes sense to break up language as a composite or mosaic of sorts (Hauser et al. 2002, Boeckx 2012) and considering the issue on a piecemeal basis.

The main take home message of this paper is thus that the rehabilitation of Lenneberg's phylogenetic thought is crucial for the evolutionary biolinguistic project, a claim that boils down to the idea that it is urgent to inject a good dose of (Owenian) homology thinking into it. The paper is organized as follows: Section 2 is a critical one, in which we document the lack of genuine homology thinking in some of the most reputed recent biolinguistic approaches to language evolution. Section 3, in turn, makes some positive suggestions about the application of homology thinking to the case of language at different levels of biological analysis. It also reflects on the landscape that such an application opens regarding the 'unique vs. shared' issue. A brief concluding remark closes the paper.

2. The Achilles' Heel of Evolutionary Biolinguistics—How Lenneberg Anticipated it

A new instrumental use of an organic structure may prove critical for the survival of a given species; yet natural evolution (not to be confounded with Natural Selection) is not about the evolution of instruments: Natural evolution is about the evolution of organic structures. An instrument is an 'intentional' object, so one to be defined attending to the purpose that it stands for—or 'intends'. But obviously enough, the intentionality of an instrument is derivative of that of a mind capable of executing such a designated purpose—or 'intention.' As a matter of fact, a long philosophical tradition, customarily traced back to Brentano's (1874) work, holds that intentionality is the hallmark of the 'mental', and that only minds are intrinsically intentional. Organic structures thus are not (cannot be) instruments, for assuming the stance that they are is tantamount to derivatively deem them intentional things, the primary source of which could not possibly be but Mother Nature. An instrumental conception of organisms and their organ constitution thus entails the underlying (anthropocentric) stance of ascribing a mind to nature (Fodor & Piattelli-Palmarini 2010, Richards 2002, 2005). Clearly, and despite the pervading instrumentalism that for centuries has been present in naturalistic thought, organs are not instruments; they are just systems, connected to and embedded within overarching systems, with characteristic activity regimes that pave the way to emergent, somehow unpredictable practical effects, given the intricacies of the internal constitution of the organism itself and of its trade-offs with the environment (Cummins 1975, Love 2007, Wouters 2003). Starting evolutionary thinking at this latter, practical interface of sorts implies locating evolutionary explanation too much ahead of where it should start.

So, while it is important to understand how the human species has taken advantage of its organic constitution along its natural history, the issue is nevertheless irrelevant when what is in dispute is how purportedly new aspects of the human natural constitution have possibly come into existence. In the case that concerns us here, all this boils down to the conclusion that deciding whether language is 'for' communicating, or 'for' thinking, or 'for' communicating or thinking about this or that, is a negligible question when debates revolve around its evolutionary origins, including its innovative or conservative character. To such an aim, the focus must rather be put on comparisons between the organic structure(s) for which the word 'language' is used as a shortcut, and other nonhuman organic structures that can reasonably be suspected of being related with it (or them) in terms of anatomy, molecular underpinnings, or physiological activity. This methodological principle was crystal clear to Eric Lenneberg in 1967, as the quote in section 1 demonstrates. Let us refer to it as 'Lenneberg's Phylogenetic First Principle'—henceforth, LPFP.

It should strike observers and practitioners of the biolinguistic program currently being developed under the habitually explicit advocacy of Lenneberg's book, that some of the most influential approaches to the evolutionary origins of language have been conducted in the last years completely sidestepping LPFP. The case of Chomsky's delimitation and compartmentalization of language for evolutionary concerns in recent works provides a dramatic illustration of this claim—see, for example, Chomsky 2013 and 2016. To start with, Chomsky symptomatically ac-

cepts the ‘communication vs. thought-related’ character of language at face value in this regard, and he concludes with the following Solomonic stance: Language is to be compartmentalized into a communication-related component and a thought-related component. On this conclusion he subsequently bases his evolutionary claim that the former, communication-related side of language—an Externalization device—belongs to a very old ancestry, so clearly is not a new language-specific component; only the latter, thought-related side—a Language of Thought—is genuinely new and purportedly the most distinctive seal of human nature. Chomsky’s evolutionary tenets are however flawed, precisely because they run, and strongly indeed, against LPFP. Let’s examine this with some detail.

Note, first, that Chomsky is delineating the evolved linguistic phenotype—both in the ‘broad’ and ‘narrow’ senses of Hauser et al. (2002)—exclusively attending to functional considerations: Language is—broadly speaking—a tool for communicating thoughts, within which the component for generating thoughts and the one for externalizing them can be safely taken apart; but above all—or narrowly speaking—language is an ‘instrument’ for thought—the word ‘instrument’ is taken from his own fragments (e.g., Chomsky 2016: 16). However, Chomsky’s move is useless as a way of identifying language as an evolved phenotype: Firstly, because pinpointing such allegedly natural functions of language, no organic structure whatsoever shows up that one can subsequently evolutionarily explain; and secondly, because the notions of ‘communication’ or ‘thought’ are being used in statements like these in merely a folk, intuitive way that hardly can serve the task of individuating a *bona fide* organic entity. Curiously enough, Chomsky is perfectly aware of the oddities of functional ascription exercises, starting with the oddity of thinking that language has a purpose (Chomsky 2016: 15, Berwick & Chomsky 2016: 63), which makes his confidence in loose functional criteria for delineating the language phenotype and making conjectures about ancestry and innovativeness even more perplexing. If this critique is on track—and we strongly believe that it is—such influential works like Berwick and Chomsky 2011, Berwick & Chomsky 2016, Bolhuis et al. 2014, or Hauser et al. 2014, even Hauser et al. 2002, to be fair, are clearly vitiated from the start, for they all rely on Chomsky’s functionally inspired conjectures about the language phenotype.¹

So, what is so vexing about functional ascription—as the likes of Berwick and Chomsky aptly acknowledge? In a nutshell, it is that organs such as, for example, bones, “do not have a single, unambiguous function”, and that “what is true for bones is also true for human language” (Berwick & Chomsky 2016: 63). An organ’s purpose may change from one to another situation, without even composing some-

¹ Chomsky’s position regarding this whole issue is, to say the least, obscure. On the one hand, his functional characterization of Externalization appears to be easily reducible to biological standards, as a system adapted to the communicative needs of Thought, the evolution of which required selecting suitably available genes, like FOXP2, according to the ‘printer’ story put forward in Berwick & Chomsky (2011)—see below. But Thought—i.e. Language proper, on the other hand, while also functionally defined, does not appear to respond to a history of adaptive evolution along similar lines—Chomsky’s preferred alternative, at least from his 1968 on, having been that it derives from a spontaneous auto-organizational process of sorts. But if so, according to most authorities (e.g., Millikan 1984), it is not clear how Thought/Language could possibly have acquired its functional credentials. This eventually leads us to our conviction that Chomsky’s ‘Thought’ is not a biologically sanctionable category, but a metaphysical one.

thing like that particular organ's functional repertoire. And more crucial to this point, an organ's purpose(s) may change from one to another species, a common observation that does not compromise that particular organ's interspecies identity. As a matter of fact, the 'homology' concept historically grew out of these kinds of observations—for example, that the forelimb may serve as a wing or as flipper,² among many other things, in different species, which justified an underlying identity concept capable of sidestepping functional considerations. When projecting this simple piece of homology thinking onto language, one easily discovers that Chomsky's uniqueness statement is, to say the least, premature, for the emergence of a new—even qualitatively—way of thinking, does not automatically entails the emergence of a new associated organic structure. For the sake of accuracy, note also that from the fact that vocal or gestural signing is widespread in the organic world, one cannot automatically derive the conclusion that language does not incorporate brand new means for doing it.

Chomsky's disregard of LPFP is not a trivial issue, for in the end it leaves the biolinguistic approach orphan of a phenotype to be evolutionarily explained. Obviously enough, the task of explaining whether it is an innovative or conservative aspect of the constitution of humans becomes vacuous in the absence of such an object. However, Chomsky is not alone in this particular side of the question. In the last years, many efforts have been directed to judge the unique or shared character of language, namely by disentangling which aspects of language can reasonably be linked with other aspects of animal cognition—see Fitch 2005, for a synthesis. Leaving aside that such comparative efforts are usually aimed at establishing connections at an observable/behavioral level—thus dealing with 'design features' or 'use' considerations, very much against LPFP, they add to this shortcoming the extra one of not being assisted by any technically established concept of 'evolutionary novelty'. We hasten to clarify that there is not a unique, consensual 'evolutionary novelty' concept in biology—see A. Wagner (2011) and G.P. Wagner (2014), for two recent non-coincidental approaches to the issue. But what is substantial to our point is that there exist some respectable definitions of such concepts. However, none of them is consistently applied in the biolinguistic approaches to the 'unique vs. shared' issue. As an illustration, let us concentrate on the Hauser, Chomsky and Fitch vs. Pinker and Jackendoff debate, which is to a great extent responsible for the incorporation of the issue into the biolinguistic agenda (Hauser et al. 2002, Fitch et al. 2005, Pinker & Jackendoff 2005, Jackendoff & Pinker 2005).

To begin with, it is worth mentioning that the contributions that articulated the debate were mostly focused on the topic of the level of abstraction that linguistic theory must adopt so that relevant comparisons with non-linguistic behaviors

² We keep off this discussion an important insight due to John Searle, who observes that functions are basically in the eye of the beholder, since deciding what a given organic structure is exactly for is clearly biased by the observer's familiarity with instruments, cultural practices, and so on (Searle 1992: 237–240). Richard Owen almost expressed the same intuition in his 1849, when he observed that it adds nothing to the characterization of the mole's forelimb to say that it is for 'digging' or for 'swimming' in the soil. For similar considerations, see also Canguilhem (1952) and, more recently, Fodor and Piattelli-Palmarini (2010), where the issue is treated under the general rubric of the 'problem of intentionality'. Incidentally, Lenneberg also suggested something along similar lines: "The human observer at times is forced to make predictions about what would be useful to a certain way of life, but predictions may be purely the result of his anthropocentric outlook" (Lenneberg 1967: 25).

can aptly be made in order to shed some light upon the issue. In fact, the main source of dissent between the contenders was that each party defended the application of a very different resolution of the linguist's lenses in conducting the enterprise. As a consequence, Pinker and Jackendoff found every reason to set apart language from any other form of nonhuman cognition/behavior, for they defended to respect the results of linguistic theory at a very fine-grained level of detail as the relevant base of comparison. In contrast, Hauser, Chomsky and Fitch concluded that language is for the most part homogenous with non-animal cognition/behavior, as one can easily appreciate by relaxing the strictures of linguistic analyses and conducting comparisons on the basis of the minimal architectural components and design specifications of the human faculty of language. We don't need to enter here into the details of the discussion that ensued. Suffice to say here that the underlying strategy that both parties shared is dubious to begin with, for it relies in a linguistic/anthropocentric stance that necessarily biases and vitiates conclusions from the outset: Namely, the acritical adoption of human language—one of the terms of comparison—as the basis for comparison at the same time. Curiously enough, Owen (1849) was perfectly aware of this potential contamination of the comparative method when he suggested that the homologies that one may reasonably conclude between organs of different species—instances of 'special' homology—might be meticulously differentiated from homologies as set by reference to an abstract, third term of comparison—instances of 'general' homology. For many, this inescapably (and fatally) leads to the original sin of Platonism. But this is not relevant here, for the right take home lesson is a different one, and Lenneberg was well aware of it: Namely, that we need neutral grounds for framing the comparative endeavor, and that such grounds must be based on independently well-established biological criteria—to repeat his own words:

[This endeavor must be based on] the relation of types of anatomical structure (including molecular structure) and physiological function (including motor coordination and sensory acuity). (Lenneberg 1967: 234)

Claims of homology or novelty are of necessity to be framed in agreement with LPFP. But this is not enough, for well-defined and sufficiently consensual 'homology' and 'novelty' concepts are also required to conduct the task on a meaningful basis. Which is another fatal flaw of the debate, as Table 1 below illustrates. As can easily be grasped, different and non-coincidental senses were used, not just by each of the contender parties—which obviously enough prevented the discussion from attaining any possible point of understanding, but also by each party along a single contribution—which prevented the debate from being fully intelligible.³

Against this background, we believe that radical changes are urgently needed in the biolinguistic enterprise in order to attain the desired convergence with evolutionary biology at large.

³ It is also a symptom of the looseness with which the discussion was conducted in the course of the debate, given the fact that no single entry in the reference list of the papers referred to any biological treatment of the subject. By 2005, however, such landmark papers like Mayr (1960), Müller & G.P. Wagner (1991, 2003) and a whole volume like Nitecki (1990), might have served this purpose

Hauser, Chomsky & Fitch		Pinker & Jackendoff	
<i>Shared</i>	<i>Unique</i>	<i>Shared</i>	<i>Unique</i>
Homolog;	Specifically adapted;	Modified;	With nothing remotely
Analog;	Uniquely adapted;	Similarities found;	similar;
Huge overlap in the mechanisms;	Lack of analog;	Homologous;	(In part) newly evolved;
Largely in place before;	Innovative;	Analogous;	Differences found;
Minor modifications;	Special;	Augmented;	Special;
Given;	Specifically evolved;	Altered;	Sui generis, specific;
Unchanged;	Qualitatively new;	Retained;	Absent in others;
Quantitatively different;	Difference of kind	Extended;	(Only) some properties in common;
Overlaps with others;		Minor extension;	Different in significant aspects
Streamlined;		Discerned in others;	
Based upon a foundation shared;		Partly overlapping;	
Built upon ancient foundations;		With other general purposes;	
Hypertrophied;		All properties in common;	
Otherwise specialized		Reminiscent of another trait	

Table 1: The multifarious folk semantics of the ‘unique vs. shared’ distinction in the Hauser, Chomsky & Fitch vs. Pinker & Jackendoff’s debate.

3. A new Heel for Achilles—With Lenneberg on our Side

LPFP precludes claims of homology from being based on either design features or functional considerations. In the previous section, we have sought to very generally justify why functional considerations having to do with ‘usefulness’ or ‘efficiency’ are pointless in this regard, but less space was devoted to design or formal criteria. Curiously enough, Lenneberg’s claim on the issue almost mimics Owen’s historical statement about what the homology concept boils down to, for he states that claims about homology were to be settled abstracting away from both formal and functional details:

Homology.—The same organ in different animals under every variety of form and function. (Owen 1843: 379)

This definition is particularly suggestive, especially when considering that in Owen’s times the most reputed method for claiming homologies was a formal one, namely the conservation of parts and patterns of correlation among them in different animals. Owen himself had to routinely recur to this method in his daily practice as a comparative anatomist, but he had the strong intuition that homologies should ultimately be based on the generative or developmental resources putatively shared by the corresponding organs (Balari & Lorenzo 2012, 2015a). It is probably not too much of a stretch to say that Owen found formal considerations rife with the same kinds of difficulties that one finds when managing with functional ones: Namely, that forms are continuous, so determining when formal varieties are tokens of the same or different formal types, again, is only in the eye of the beholder. Pinpointing generative/developmental criteria as a neutral ground for deciding anatomical sameness was certainly within the purview of 19th century anatomists, even if the adequate operationalization means were still lacking.

The previous comments amount to the conclusion that anatomical homologies ultimately are to be resolved on developmental grounds, which nowadays

mostly—but not exclusively—means on molecular grounds (G.P. Wagner 1989). Subsection 3.1. below is devoted to introducing the prospects of such a project in the case of language and points to some tentative conclusions regarding the ‘unique vs. shared’ issue that, we think, can plausibly be drawn at this point in time. After this, subsection 3.2 reflects on how one should conceptualize the functional/physiological level of analysis, also pinpointed by Lenneberg, in order to operationalize it for the same goal.

3.1. *Anatomical/Molecular Structure*

Individuating organic systems is not an easy task. Yet, it is a crucial one for deciding the case of the putative novelty of a particular such system. Actually, having a robust rationale for the individuation of organs is part and parcel of the attribution of a unique or shared identity of a particular organ at a given evolutionary time. This is, for example, the route recently taken by Günter P. Wagner, whose homological theory primarily relies on the distinction between the ‘character identity’ and the ‘character state’ concepts (G.P. Wagner 2014: 51–54): A character identity refers to an underlying ‘sameness’ to different organ tokens, while character states refer to the more or less varying ways in which these organ tokens actually surface. As stated in the previous formulation, a given character identity is not something that one may expect to be open to direct inspection: It is an ‘underlying’ property, not a ‘superficial’ one, contrary to formal or functional traits—thus in agreement with the classical, Owenian homology concept discussed above. According to G.P. Wagner (2014: Ch. 3), what makes different organ tokens of the same organ type is their sharing an underlying Character Identity Network (ChIN), which he defines as a reiterative pattern of interactions between genetic sequences—and products thereof—that interfaces with, on the one side, positional information provided by inductive signals, and, on the other side, ‘realizer’ genetic machinery, the activity of which brings about alternative character states in different developmental scenarios. The ChIN concept thus provides an explanation for the developmental individuality of a body part, that is its ability to express different sets of realizer genes than other body parts. Diverse illustrations are provided by G.P. Wagner (2014), which underpin traditional homological attributions—for example, fin/limb identity (Owen 1849, G.P. Wagner 2014: Ch. 10), but put into question some others—like the one that putatively holds of different vision organs (Gehring & Kazuko 1999, G.P. Wagner 2014: 111). In any event, it is the big picture, not particular applications, which is relevant for our present concerns.

It is good news that G.P. Wagner’s model locates us on a developmental terrain, for knowledge about the developmental and, ultimately, genetic basis of language, while still limited, has dramatically increased in the last years, thanks to the window provided by congenital language impairments—which already were one of Lenneberg’s focuses of attention (Lenneberg 1967: Ch. 6). We know now of the central role of the *FOXP2* hub gene in the sustained regulation of genetic activity that leads to the configuration of a complex neural circuitry that comprises parts of the basal ganglia, the cerebellum, the frontal cortex, and re-entering tracts of fibers connecting them (Lai et al. 2001, Enard et al. 2002, Lai et al. 2003, Liégeois et al. 2003, Enard et al. 2009, Reimers-Kipping et al. 2011; see Newbury et al. 2010, Enard

2011, Preuss 2012, and Graham & Fisher 2013, for some state-of-the-art reviews). Besides, we also know how *FOXP2* promotes neural differentiation at these particular sites by interacting with the retinoic acid signaling pathway, which regulates neuronal migration (reducing it) and neurite outgrowth (increasing it), two key processes for neural circuit formation (Vernes et al. 2011, Devanna et al. 2014, van Rhijn & Vernes 2015). Progress has also been made in the identification of genes targeted by *FOXP2* during the corresponding developmental loop, which reasonably enough contribute either to keep it active or to realize the form/function specificities of the resulting human characteristic circuitry (Johnson et al. 2009, Konopka et al. 2009, Vernes & Fisher 2009, Newbury & Monaco 2010, Roll et al. 2010, Vernes et al. 2011, Konopka et al. 2012, Ayub et al. 2013, Chiu et al. 2014, Rodenas-Cuadrado et al. 2014, Webb 2015). Finally, important insights have been gained with regard to enhancers and protein regulators—for example, SUMO proteins—of *FOXP2*'s own activity (Bonkowsky et al. 2008, Becker et al. 2015, Estruch et al. 2006, Becker 2016, Torres-Ruiz et al. 2016, Usui et al. 2016).

Needless to say, what we at present have at our disposal is certainly only a small fragment of a very intricate net of molecular products and interactions, to be hopefully more extensively unveiled in the years to come—for a visualization of its present state, see Konopka et al. (2012: 619; fig.6). In any event, what we already have starts to look very much like a Wagnerian ChIN, as figure 1 tries to illustrate. The skeleton of the figure is taken from G.P. Wagner (2014: 97; figure 3.8), we simply super-add a few representative data from the sources referred to in the previous paragraph.

Let us stress that the hypothesis above amounts to the tenet that *FOXP2* is part of a regulatory network that developmentally individuates parts of the brain, which, in humans, correlates with/embodies the language capacity. Assumedly, such a hypothetical network still waits for stronger experimental support than hitherto available; yet we contend that known putative fragments may already serve the task of guiding a homological enterprise. Regarding this enterprise, it is also crucial to keep in mind that such a task is not merely one of detecting gene names here and there, but of witnessing relevant interactive patterns between reasonable orthologs and related materials.

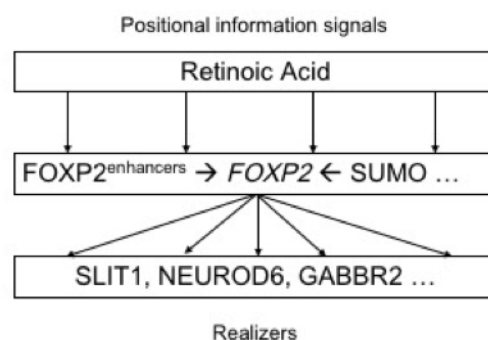


Figure 1: A first take on the language ChIN. The hub *FOXP2* gene is represented in the image as interfacing key positional clues and a complex machinery of self-sustaining or realizer molecular stuff.

The previous comment also points to the reason why we believe that the ChIN concept provides a more powerful tool for conducting such a homological program than the closely related, yet different ‘deep homology’ one, which refers to extremely conservative genetic sequences that demonstrably have a key role in the making of organisms (Shubin et al. 1997, 2009; see Fitch 2011 and Scharff & Petri 2011, for its application to the case of language). Clearly enough, deep homologies reveal non-trivial evolutionary relations; yet, they clearly do not manage by themselves to support claims of ‘sameness’, like the ones that the ChIN concept is aimed at capturing. Deep homology concerns the natural proclivity to re-deploy resources, but this is so even in cases where, considering the whole context, resources have been recruited for the making of (more or less radically) different organs. Besides, ChINs only make sense when what is at stake is the individuation of organs, while deep homologies liberally apply at lower levels of analysis—for example, protrusions and other intermediate structures, particular aspects of an organ’s composition, etc. (G. P. Wagner 2014: 36).

Partial as the available information surely is about the putative ChIN represented in figure 1, we however insist on the claim that it is rich enough to start carrying out a *bona fide* homological project as regards human language (Balari & Lorenzo 2015b). Such a claim is partially based on our conviction that, for the first time, an amenable theoretical model exists to confidently guiding the task, but also on the fact that abundant comparative data already exist, from which some preliminary conclusion can already be achieved (Webb & Zhang 2005, White et al. 2006, Fisher & Scharff 2009, Konopka & Geschwind 2010, Scharff & Petri 2011, Fontenet & Konopka 2014). To cite but a few, orthologs of *FOXP2* have been exhaustively studied in organisms such as as the fly—(*d*)*FoxP* (DasGupta et al. 2014, Lawton et al. 2014, Mendoza et al. 2014), the bee—*AmFoxP* (Kiya et al 2008), zebrafish and medaka—*foxP2* (Bonkowsky & Chien 2005, Shah et al. 2006, Itakura 2008), the bat—*FoxP2* (Li et al. 2007, Chen et al. 2013, Vernes 2017), and the mouse—*Foxp2* (Ferland et al. 2003, Lai et al. 2003, Shu et al. 2005, Enard et al. 2009, Enard 2014, Fujita & Momoi 2014, Schreiweis et al. 2014, Medvedeva 2015, Castellucci et al.

organism	genetic proxy	loci of expression
<i>Drosophila melanogaster</i>	(<i>d</i>) <i>FoxP</i>	Protocerebral bridge (PB) (\approx Striatum) / Central complex (CX) (\approx Basal ganglia) / Optic, glomeruli
<i>Apis mellifera</i>	<i>AmFoxP</i>	Optic lobes / Central Complex / Dorsal lobes / Protocerebral lobes (connected by PB)
zebrafish	<i>foxP2</i>	Telencephalon / Diencephalon / Cerebellum / Hindbrain / Tectum / Retinal ganglion cells / Spinal cord
echolocating bats	<i>FoxP2</i>	Suprageniculate nucleus (SG) / Anterior cingulate cortex (ACC) (\approx BA 32, 33, 24)
mouse	<i>Foxp2</i>	Cerebral cortex / Thalamus / Cerebellum / Spinal cord

Table 2: Some preliminary bases for a putative cross-species ChIN comprising language.

2016, Chabout et al. 2016). Plotting observations made in these papers, results in an anatomical continuum that comprises neighboring or equivalent structures to the ones routinely pinpointed as correlates of *FOXP2* expression in the case of humans, as reflected in table 2.

In any event, the most dramatic results of this comparative enterprise have been provided to date for the case of songbirds. More concretely, the role of the *FOXP2* transcription factor in the development and activity of the brain of these avian species has been firmly established (Haesler et al. 2004, Teramitsu et al. 2004), and a structure considered to be equivalent to (parts of) the basal ganglia (Area X) has been pinpointed as the one with which *FOXP2* more strongly correlates (Haesler et al. 2007, Phillmore et al. 2014). Moreover, the role of retinoic acid as a key inductive signal in the development of this and some closely related structures (e.g., HVC, RA, IMAN) was known even before (Denisenko-Nehrbass et al. 2000, Denisenko-Nehrbass & Melo 2001, Roeske 2010, Roeske et al. 2014). Finally, an impressive amount of information regarding active (putatively realizer) genes of the referred structures has been recently provided, which strongly supports the homological relation with the human brain's candidate correlates (Pfenning et al. 2014): Namely, 78 genes are identified as active both in the songbird Area X and the human putamen, 40 in the birdsong RA and the surroundings of the human central sulcus, and an unspecified number (but in the order of the tens) in the birdsong RA and the human laryngeal motor cortex (LMC). Figure 2 offers a visualization of these results.

The resistance to admit all this background as informative of cases of *bona fide* homology strikes us as surprising. In this regard, Berwick's and Chomsky's position is paradigmatic: On the one hand, they agree that such data point to a case of deeply shared evolutionary history; on the other hand, they believe that it only touches the (peripheral) Externalization component of human language. Language 'proper'— that is the generative engine in charge of composing unboundedly internal expressions (aka bare thoughts)— has nothing to do with the kinds of molecular and anatomical findings that we have been reviewing (Berwick & Chomsky 2011, Berwick & Chomsky 2016, Chomsky 2016). Their stance is how-

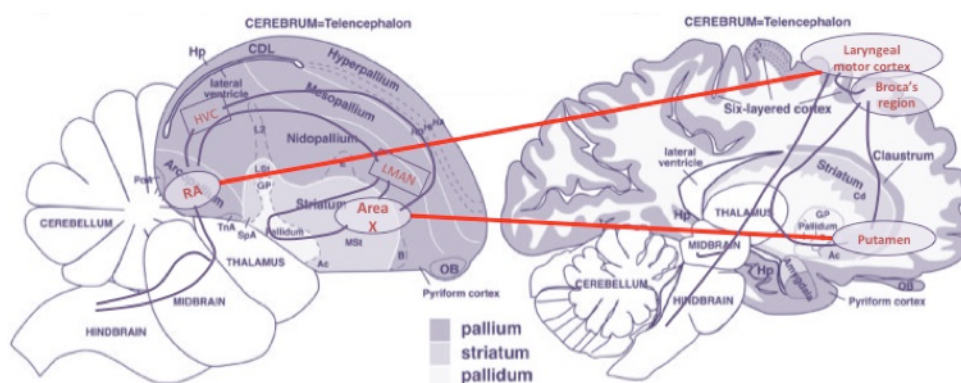


Figure 2: Some homological relations between the birdsong and the human brain, well established on developmental grounds. Illustration reproduced from Balari & Lorenzo (2015b: 12; fig. 4).

ever deceiving, for some animal models make us suspect that the cognitive import of the putative ChIN that we endorse is, as a matter of fact, orthogonal to the externalization/thought distinction. For example, Schreiweis et al. (2014) conclude that, in mice, it correlates with the declarative vs. procedural styles of learning and processing, and Chandrasekaran et al. (2015) corroborate that this appears to be also the case in humans.

But let us put aside these kinds of functional considerations for the time being. Berwick's and Chomsky's position is still, in all likelihood, conceptually unsound: Their discriminating between an externalization-related component and an internal thought-related component within the faculty of language, is merely made by fiat—that is, independently of any biological criterion. Ultimately, it conspicuously runs against Lenneberg's LPFP. But note that even if the biolinguistic claim were admissible that language is an instrument for thought—as Chomsky believes it to be—it still is without any biological motivation that an instrument for thought cannot be the same instrument that different animals use for, say, communication. In any event, such are bold claims, made without caring about the level(s) of organic activity on which claims of homology—or of lack thereof—can legitimately be made. We presently turn to this issue.

3.2. *Physiological Function*

Biological Foundations of Language can be safely described as the best compendium of neurophysiological knowledge concerning language, for 1967. One must not forget that, at the time of writing, the data coming from neuroscience Lenneberg had at his disposal had not yet gone much beyond the pioneering work of Edgar Adrian in the late 1920s.⁴ No wonder then that our vindication of Lenneberg in this context will have little to do with empirical findings. As it was the case in the previous subsection we will focus on questions of method and insight.

If we were to highlight what in our opinion are the most relevant aspects of Lenneberg's stance with respect to the role of neurophysiology for the case of language, we think we would underline the following:

- (i) Lenneberg's conviction that gross differences in cognitive capacities would translate to relatively small differences in structure, but would correlate instead with differences in the way a number of fairly well-preserved (i.e. homologous) structures interact.
- (ii) Lenneberg's conception of biolinguistic explanation.

As for the first, we will have little to say, since this is today considered common knowledge in the field of neuroscience: "The main difference between brains of simple and complex animals is merely the number of neuronal loops that link

⁴ A few examples will suffice. The Hodgkin and Huxley model of the action potential was first presented in 1952, but it remained a model for at least 20 years; the first experiments by Hubel and Wiesel on the visual cortex of the cat were first presented in 1962, but these just define a research project that, again, spans for more than 20 years; finally, the Society for Neuroscience was only founded in 1969 (<https://www.sfn.org/About/Mission-and-Strategic-Plan>; accessed 16/07/2017). These and many other examples can be found in any contemporary neuroscience book; see Churchland (1986), Churchland & Sejnowski (1992), Rieke et al. (1997), Craver (2007). Also see Arbib (this issue) who makes the same point.

the outputs to the inputs” (Buzsáki 2006: 32; see also Schneider 2014). To be sure, another point on which everyone appears to agree is that we want to understand brain ‘computation’ and that this is impossible without knowing something about the basic connectivity of the brain (Eliasmith & Anderson 2003: Ch. 1, Buzsáki 2006: Ch. 2, Seung 2012 for an introduction to ‘connectomics’). Lenneberg did not express it with these words, but it is obvious that this is what he meant when he wrote that “[a]ll aspects of behavior may be considered to be based upon modulation of activity in neuronal nets” (Lenneberg 1967: 215). The crucial point however is the role Lenneberg attached to neurobiological descriptions in accounts of human linguistic capacities, since it is pretty clear that for him a complete characterization of the underlying mechanisms constituted a full-fledged explanation of the phenomena in question. This idea permeates the whole book, but perhaps the most illustrative quotation is this:

It would be presumptuous to try to explain the nature of the innate events that control the operations of language. We may, however, assume that mechanisms are involved, such as (1) the modulation of firing characteristics of nerve cells; (2) the triggering of temporal patterns in neuronal chains; (3) the modulation of oscillatory characteristics of endogenous activities; and (4) the production of spreading of disturbances. These are some of the components of the automaton. How these phenomena interact to elaborate language remains a mystery.

(Lenneberg 1967: 221)

In the purest Cartesian tradition (note his reference to the automaton), Lenneberg’s conception of explanation is mechanistic through and through. But why should we bother to emphasize this point?—Some may ask: Is it not the case that explanation in the biolinguistic tradition has always been mechanistic? Well, not really (or not quite), we would contend, which obviously deserves some elaboration and to which we will devote the remainder of this section.

The issue is a delicate one. And it is because, although it is generally assumed that cognitive science/psychology and (bio)linguistics have been sailing in the same boat for the last sixty years, it is certainly not the case that both have adopted the same explanatory standards.⁵ Take the case of cognitive science first. In this field, the debate has mostly centered around Jerry Fodor’s notion of a ‘special science’ and the specific explanatory requirements that, according to him, these sciences impose (see Fodor 1965, 1968, 1974, 1975: 1–26, 1997). In essence, Fodor’s model of explanation is a two-step account, where the first step (the phase one explanations of Fodor 1965) is to be set in terms of functionally characterized notions like ‘beliefs,’ ‘desires,’ and so on, complemented by research “directed towards determining the nature of the mechanisms whose functional characteristics phase one theories specify” (Fodor 1965: 176). We have dug into the roots of the issue, because Fodor’s early writings already delineate a view in which functional and mechanis-

⁵ Our use of the labels ‘cognitive science,’ ‘psychology,’ and ‘biolinguistics’ is merely instrumental and certainly not intended to capture the complex geography of the field. The intended idea, as it will become clear presently, is that Chomsky’s position needs to be set apart from mainstream approaches to cognition, hence, to simplify further, in the text we will as of now just confront ‘cognitive science’ with ‘biolinguistics’.

tic explanations are presented as different, albeit complementary, things and, consequently, autonomous from each other. The autonomy thesis erected by Fodor in 1965 and later propped up in Fodor (1974, 1997) is one of the dominant perspectives in contemporary cognitive science generically known as ‘functionalism’.⁶ In a nutshell, functionalism is the idea that cognitive systems are to be analyzed at a functional level that is not reducible to the neurophysiological level, mostly because macrolevel functional descriptions may be multiply realized at the microlevel, rendering any attempt to reduce the former to the latter impossible or, at least, uninformative and, therefore, not really explanatory; see, in addition to the already cited works, Putnam (1975) for a construction of the argument parallel to Fodor’s, and Polger & Shapiro (2016) for a detailed exposition of the issues involved. The net effect of this perspective is the well-known attitude observed within cognitive science that research can proceed without paying too much attention to what is going on in the neurosciences. But the historical reasons of such a divorce run deeper and stem from the more or less tacit acceptance by most cognitive scientists of the deductive nomological model of explanation articulated by Hempel & Oppenheim (1948) coupled with the unity of science view of Oppenheim & Putnam (1958). According to this model, genuine scientific explanation amounts to reduction of (the laws of) some higher-level science to (the laws of) a lower-level science, where the most fundamental science is physics, such that, eventually, all science would be reduced to physics. This is a somewhat caricatured exposition of the model, which doesn’t affect the fact that it has been taken very seriously by many philosophers and cognitive scientists, in particularly those within the eliminativist camp (Churchland 1989, especially chapters 1 and 5, Bickle 1998, 2003). Thus, functionalism may be understood as a movement within cognitive science which, feeling uncomfortable with the prospects of elimination wielded by reductionist models of explanation, opts for a middle-ground position accepting a weaker (non-eliminativist) version of reduction that supposedly would keep it away from the dangers of (metaphysical) dualism (see Kim 2005, for a paradigmatic exercise along these lines).

It is interesting to notice to what an extent has Chomsky remained alien to these debates. Indeed, to great disappointment for many functionalists (e.g., Lycan 2003), he has mostly kept a (censoring) silence towards functionalist positions only broken to effectively dismantling it (Chomsky 2003, also 1997: 29–31). And for good reason: Chomsky’s thought may be subject to many different criticisms but it certainly cannot be charged with incoherence, and one of the most salient (and often misunderstood) of Chomsky’s philosophical positions is the one summarized by the following quotation: “Lacking a concept of ‘matter’ or ‘body’ or ‘the physical,’ we have no coherent way to formulate issues related to the ‘mind-body problem’” (Chomsky 1995a: 4–5).⁷ As a consequence, Chomsky’s ‘naturalism’ concerning the mind is at most homophonous with the ‘naturalism’ typically observed within

⁶ “Functionalism is a mess”, Polger (2004: 71) observes, but as far as the argument in the text is concerned, little hinges on the nuanced variety of different functionalisms currently en vogue. See Polger (2004) for a taxonomy.

⁷ The most explicit elaboration of this position by Chomsky goes back to the late 1980s through the 1990s, roughly in parallel to the first steps of the Minimalist Program (Chomsky 1995b)—presumably not a coincidence, but it certainly could be identified in most of his more philosophical works prior to that; see Chomsky (2000) for a collection of texts where the idea is articulated, and Poland (2003) for an illuminating analysis.

Anglo-American philosophy of mind (Dennett 2017, for the most recent example), as it is not an exercise of ‘naturalization’ but simply the assumption that minds are natural objects and therefore constrained by the very same principles applying to other entities of the world, whatever they are.⁸ Only in this context can Chomsky’s iterated affirmation that eliminativism as a doctrine is not really intelligible be understood (e.g., Chomsky 2000: 25, among many other sources). It is not intelligible because, if we interpret Chomsky’s naturalism correctly (and we think we do), the kind of reductive eliminativism⁹ so feared by the likes of Fodor and Putnam only makes sense when relying on the Oppenheim-Putnam Unity of Science framework for explanation, which is not Chomsky’s. His framework is Cartesian (i.e., mechanistic) from root to branch, with the only proviso referred to above concerning the status of the ‘physical’—just like Lenneberg’s, by the way.

The biolinguistic tradition thus appears to converge with a new wave of mechanistic philosophy of science, whose foundational text is Machamer et al. (2000) and which has given rise to a number of relevant monographs (Craver 2007, Bechtel 2008, Craver & Darden 2013, Piccinini 2015).¹⁰ The idea behind mechanistic explanation is a priori fairly simple, but actuality suggests that it is not as easy to apply consistently as it seems. Take, for example, a standard definition of mechanism like the following:

Mechanisms are how things work, and in learning how things work we learn ways to do work with them. Biologists try to discover mechanisms because mechanisms are important for prediction, explanation, and control.

Biologists seek mechanisms that produce, underlie, or maintain a phenomenon.¹¹

(Craver & Darden 2013: 15)

As the definition suggests, the basic methodology of mechanistic explanation consists in identifying a phenomenon we want to explain—say, Long-Term

⁸ See, in particular, Chomsky (2000: Ch. 4). In a slightly different context we adopted the same strategy in our attack to functionalism in Balari & Lorenzo (2015a). As a matter of historical detail, however, we are not entirely sure that the Newtonian revolution had the effect of turning “Newton’s anti-materialism” into “scientific common sense” (Chomsky 1995a: 5), simply because ‘immaterial’ at the time had a variety of meanings, ranging from ‘not directly perceptible’ to ‘poorly understood’, all of them falling within what was considered to be ‘natural’ (vs. the ‘supernatural’); see Balari & Lorenzo (2013b) where some illustrative examples taken from the work of Richard Owen and Michael Faraday, for example, are presented.

⁹ The epithet ‘reductive’ is pertinent here, because not all varieties of eliminativism are reductive. Thus, for example, Churchland’s (1989) or Stich’s (1983) eliminativism towards folk-psychological categories is not motivated by the idea that these will eventually be reduced to neurophysiological categories but by the conviction that folk psychology is nothing but a “culturally entrenched theory” (Churchland 1989: 17) that will vanish as science progresses; similarly (and for similar reasons), we have exhibited our eliminative tendencies towards teleological functions in Balari & Lorenzo (2010).

¹⁰ Perhaps not surprisingly, no tradition acknowledges the other but both locate their historical roots in references to Cartesianism (cf. Chomsky 1966, Bechtel 2008: Ch. 1, Craver & Darden 2013: Ch. 1).

¹¹ “We want to discover how actual systems work” (Chomsky 1997: 31). “While teleology seeks to answer a why-is-it-there question by answering a prior what-is-it-for question, functional analysis does not address a why-is-it-there question at all, but a how-does-it-work question” (Cummins 2002: 158).

Potentiation (LTP), to take a classical example—and describing the mechanism that produces, underlies or maintains it—in the case of LTP, the release of glutamate from a pre-synaptic neuron that results in changes in a post-synaptic neuron; see Craver (2007: 65–72), for details. Essentially, then, the strategy involves identifying a series of “entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions” (Craver & Darden 2013: 15). It would therefore seem that there’s nothing new under the sun (and, in some sense, there isn’t) because this looks very much like the kind of ‘functional analysis’ that, for example, Fodor (1965) and Cummins (1975, 1983) claim is an integral part of a complete psychological explanation. The (crucial) difference has to do with how the relevant levels of analysis are conceptualized in one and the other approach. Remember that Fodor justified a two-level approach in order to argue for the autonomy of functional analysis from mechanistic explanation and that we traced this back to Fodor’s more or less tacit acceptance of a conception of levels based on the unity of science view. What Fodor failed to see¹² is that rejecting autonomy is not an argument for reductionism, it has never been, because the conception of ‘level’ that is predominant in the mechanistic tradition has nothing to do with the Oppenheim-Putnam model and, de facto, renders the classical idea of reduction nonsensical (as Chomsky would probably put it). Levels of mechanisms are not levels of science, because they involve a kind of part-whole relation in the sense that they are levels of behaving components that, in turn, may be identified as mechanisms, and therefore the part-whole relation makes only sense in the context of the mechanistic decomposition, often failing to correspond to the spatial boundaries one identifies in a purely mereological analysis; see Craver (2007: Ch. 5) and Craver (2015) for discussion and examples.

And thus we come to one of the cruxes of the matter, since it is our contention that most self-declared biolinguistic approaches—but according to our exegesis, closer to the cognitivist orthodoxy; see fn. 4—have systematically misapplied the notion of ‘level’ in their attempts at solving the unification problem, in Chomsky’s (2000: 103) sense.¹³ Take the case of David Poeppel’s proposals as to how to carry out the program originally delineated by himself and David Embick (Poeppel & Embick 2005, Poeppel 2012). In his paper, Poeppel argues, convincingly, that most current research in cognitive neuroscience is wrongheaded because it insists on drawing maps of the brain, associating functions to specific areas, when “localization and spatial mapping are not explanation” (Poeppel 2012: 35). As an alter-

¹² The case of Cummins is a bit more elaborate and a close examination would take us too far afield; see Piccinini & Craver (2011) for discussion.

¹³ Chomsky has not been very specific about what he means by ‘unification’, but in Chomsky (1993: 46) he associates the concept with the question “How can organized matter have [the properties of mind identified by the Cartesians]?” so we believe it is safe to identify ‘unification’ with what Craver (2007: Ch. 7) terms ‘interlevel integration’ (roughly, identifying an item as a component of a higher-level mechanism and, in turn, identifying the lower-level mechanisms that constitute that component qua mechanism). Also, although Chomsky sometimes uses the word ‘reduction’ when considering one of the possible consequences of unification, he cannot possibly mean ‘reduction’ in the classical sense and we take it that his use is roughly synonymous to what Craver calls ‘intralevel integration’ (roughly, integration of different disciplines into an encompassing discipline); in fact, one of the examples Chomsky usually refers to (the incorporation of biology within known biochemistry) is better interpreted in this sense (Craver & Darden 2013).

native, Poeppel makes a case for what he calls addressing the ‘mapping problem’, which he defines as the

[...] investigation of the (ultimately necessary) *formal relations* between two sets of hypothesized inventories, the inventory constructed by the language sciences and that constructed by the neurosciences.

(Poeppel 2012: 35; emphasis in original)

To the extent that the meaning of the phrase ‘formal relations’ remains suitably vague, Poeppel’s approach may count as mechanistic (as opposed to reductionist), but it is not obvious that he succeeds in really dismissing the classical view (if this is really his goal).¹⁴ The main problem lies in Poeppel’s invocation of David Marr’s levels—which has become standard in cognitive science—as the guiding model to achieve explanatory theories. But appealing to Marr’s levels can only generate a paradox, because Marr never believed in the explanatory power of neuroscience,¹⁵ while Poeppel is clearly assuming otherwise. To be sure, Marr’s model of explanation could be better characterized as intentional, even teleological, given the preponderance of ‘why’ components as opposed to the ‘how’ components typical of mechanistic explanations (Shagrir 2010), and therefore, without actually denying that the kind of computational analysis that Marr proposes may play some explanatory role, it cannot be the central element of any true computational mechanistic approach (Piccinini 2007, Shagrir 2010, Piccinini & Craver 2011, Piccinini 2015). More to the point, Marr’s ‘computational’ and ‘algorithmic’ levels are not levels in the up-down interpretation that (almost) everybody gives to them (e.g., Poeppel 2012: 52), but rather slightly different perspectives from which a particular mechanism can be looked at and, hence, not actually autonomous from the ‘implementation’ level nor from each other, as Marr suggested (see Piccinini & Craver 2011: 302–303 and Piccinini 2015: 97–98, for discussion and further justification). Again, this is not to deny that a computational analysis may be relevant, but as we will suggest presently it will only share some elements with that of David Marr, namely those that clearly involve a breakup of the computational mechanism into parts, together with an assignment of functions and organization to those parts that is capable of showing that the capacities of the system are an effect of how the parts perform their activities (Piccinini 2007, 2015).

The issue of Marr’s levels has percolated to other approaches trying to fulfill Poeppel’s program. For example, Boeckx and Theofanopoulou (2014: 405 and figure 1) propose a stratified approach that supposedly bottoms out at the ‘genome’ and tops off at the ‘phenome’ or phenotypic level, spanning a number of intermediate levels like the ‘connectome’ (the set of neural connections), the ‘dynamome’ (the linking of brain connectivity with brain dynamics), and the ‘cognome’ (roughly Marr’s

¹⁴ For example, the kinds of relations typical reductionist approaches describe between theories at different levels are inferential (i.e., formal; Craver 2005). Also, while Poeppel often appears to be arguing against reductionism (e.g., Poeppel 2012: 36, 51, 52), his putative attacks are lukewarm at best, as he mostly seems in fact to be refurbishing Fodor’s autonomy thesis by vindicating the equal status as fundamental science of cognitive psychology with respect to neuroscience.

¹⁵ “The key observation is that neurophysiology and psychophysics have as their business to *describe* the behavior of cells or of subjects but not to *explain* such behavior” (Marr 1982: 15; emphasis in original). By the way, Chomsky has also expressed his reservations to finding points of contact between his approach and Marr’s (Chomsky 1997: 23).

computational levels; Poeppel 2012: 35). Consider the case of the ‘connectome’ and the ‘dynome’, for example. These are clearly not levels in any possible sense, since, as Kopell et al.—the inventors of the term ‘dynome’—observe:

What is needed is not only *what* is connected, but *how* and in what directions regions of the brain are connected: what signals they convey and how those signals are acted upon as part of a neural computational process. (Kopell et al. 2014: 1319; emphasis in original)

Thus, in a typical mechanistic fashion, we identify the connections (parts) and the signals and operations over signals (activities) these parts perform, and it is this organization together with its behavior in specific circumstances what makes this the mechanism underlying a phenomenon, not their position in a predefined level. In fact, talk of levels defined a priori is useless, because, as pointed out by Craver (2007: 191), this has to be solved on a case-by-case basis—what is explanatory relevant for each phenomenon “cannot be read off a menu of levels in advance.”

Failure to carry out a mechanistic analysis may result in misrepresenting Lenneberg’s prediction that “it is not possible to assign any specific neuro-anatomic structure to the capacity for language” (Lenneberg 1967: 72) in the sense that we “need to think of language-related tasks as ‘whole-brain’ affairs” (Boeckx & Theofanopoulou 2014: 411). This, we surmise, is inaccurate and a mere side effect of the fact that, more often than not, “the components picked out in a mechanistic decomposition fail to correspond to paradigmatic entities with clear spatial boundaries” (Craver 2007: 190), because the unifying principle is organized behavior or, in other words, “the peculiar way in which the various parts of the brain work together” (Lenneberg 1967: 72). Part of the problem stems, no doubt, from lack of consensus—and, we should add, accuracy—in the characterization of what constitutes the ‘linguistic cognome’, to use Poeppel’s (2012) expression and diagnostic, which may be worked out also by applying Poeppel’s recipe of ‘radical decomposition’ in the characterization of the phenomena liable to mechanistic analysis, ‘language’ being just an umbrella term ranging across several phenomena, each subserved by a manifold of (possibly overlapping) underlying mechanisms.

Notwithstanding, Poeppel’s strategy, promising as it is, still faces in our opinion a more recalcitrant problem: the problem of computation (Balari & Lorenzo 2016). Few would challenge today the contention that the foundational hypothesis of cognitive science is that cognition is computation.¹⁶ Lenneberg, for one, already foresaw that the core of an explanatory account of language would necessarily incorporate a computational account of the biological operations involved (physiological function)¹⁷—hence our digression above to reach this point. Unfor-

¹⁶ Some do, for example Tim van Gelder (van Gelder 1995, 1998), but, as shown by Kaplan & Craver (2011), the kinds of models championed by dynamicists are holistic models that describe the behavior of some complex system without actually paying attention to how it does work and are, therefore, nonmechanistic.

¹⁷ This point is more explicitly expressed by Lenneberg in his 1969 paper than in the 1967 book, thus:

it is [...] reasonable to assume that individuals who speak Turkish, English, or Basque (or who spoke Sanskrit some millennia ago) all have (or had) the same kind of brain, that is, a computer with the same operating principles and the same sensorium; (Lenneberg 1969: 640)

unately, paraphrasing John Haugeland (2002: 160), we don't seem to know anymore what computation really is. Which probably is but the tip of the iceberg of our poor current understanding of cognition at a functional/physiological level. Computation, to be sure, is a complex notion, susceptible to many different interpretations and formalizations (Smith 2002, for at least seven of these) and therefore we still need to find an answer to the question: "What *type* of computation is cognition?" (Smolensky & Legendre 2006: 5; emphasis in original). But the question itself may be deceiving, for we do not even know whether computation exhausts cognition. So a first, more urgent question would perhaps be: "What type of cognition is computation?" Some higher-order notion should come to the rescue here, a natural (cover) kind of sorts for all types of cognition—computational or otherwise. Some insistently claim that the 'dynamical system' concept may do the job (see, for example, Wheeler 2005). But if so: What type of dynamical system is a computational system? For many, the answer is straightforward: Dynamical computational systems are those that specifically feed on units that matter for their informational value, not just for their metabolic or energetic import. But this just introduces us into the not less slippery vocabulary of vehicles, symbols, representations, and so forth (Balari & Lorenzo 2016), the prospect of naturalizing which is for many beyond the limits of the human science-forming capacity.

Even putting aside most such complicating factors, the most plausible formalization of computation capable of accounting for higher cognitive processes, digital computation, doesn't appear to match what we know so far about what is going on in the brain. In other words, neural computation (if it is computation at all) appears to be *sui generis* (Piccinini & Bahar 2013), and at present we do not have a comprehensive notion of computation encompassing the traditional view and the kind of computational activity that brains are presumed to perform—computational neuroscientists simply assume that nervous systems compute, no one has ever proven that this is so (Piccinini & Shagrir 2014). In any event, it might be the case that a concept of computation not very different from the traditional one will be suitable enough for the particular case of the computation of internal linguistic expressions, considering that this is a task in which the subtle and precise synchronization processes with the complex ongoing flux of environmental stimulation, which for some marks an upper limit for classical computation (Wheeler 2005), do not dramatically arise. So far, however, all this is beyond anyone's guess.

We raise these issues hopefully not for provoking a paralyzing effect, but to caution against an excessively enthusiastic reading of certain recent proposals concerning the computational character of brain oscillations (e.g., those of Murphy 2015, 2016) which do not seem to have taken into account the complications we just alluded to. To repeat, this is not to deny the potential relevance of brain oscillations in an eventual account of neural computation, but evidence so far is only correlational, in the sense that oscillations do play some role in linguistic tasks (e.g., Lewis et al. 2015, Lewis & Bastiaansen 2015, Ding et al. 2016), but we have so far been unable to disentangle the computational role they purportedly play. Compared to the bulk of data coming from the neuroscience camp, relatively little effort is being devoted to articulate detailed computational analyses capable of "[challenging]

and "[t]he human brain is a biochemical machine; it computes the relations expressed in sentences and their components" (Lenneberg 1969: 642–643).

neurobiologists to define and characterize the neural circuitry that can underpin [them]”, as Poeppel (2012: 52) would put it. The theory of computation is our main tool to carry out this project as it makes it possible to construct hypotheses and to identify constraints under the assumption that, if brains compute, then cognition is tractable (Frixione 2001, van Rooij 2008, Balari & Lorenzo 2013a). An example of this could be the proposal articulated both by Gallistel & King (2009) and by Balari & Lorenzo (2013a), each based on different grounds, that a basic component in the architecture of the computational system would be a memory workspace, given the inherent complexity of certain tasks carried out both by humans and other animals. A project not too detached from Lenneberg’s conjecture that

The cognitive function underlying language consists of an adaptation of a ubiquitous process (among vertebrates) of categorization and extraction of similarities. (Lenneberg 1967: 374)

4. Concluding Remarks

In *Language and Thought*, Chomsky conjectures that if the human cognitive system was

embedded in different performance systems in some hypothetical (perhaps biologically impossible) organism, [lexical items] could serve as instructions for some other activity. (Chomsky 1993: 48)

In this paper we have tried to show that the research program delineated by Lenneberg, with his views on phylogenetics and mechanistic explanation, already contains the seeds for showing that Chomsky’s hypothesized organism is not only not biologically impossible but that it may have been, and may be, quite actual. Bad times for human uniqueness? We believe so. In any event, not worse than 50 years ago, when Eric Lenneberg had already broadcasted it.

References

- Anderson, Stephen R. & David W. Lightfoot. 2002. *The Language Organ: Linguistics as Cognitive Physiology*. Cambridge: Cambridge University Press.
- Arbib, Michael A. 2017 [= this issue]. “Language and Brain: Developmental Aspects”: Eric Lenneberg at the Neurosciences Research Program in 1972. *Biolinguistics* 11(2).
- Austin, John L. 1962. *Sense and Sensibilia*. Oxford: Oxford University Press.
- Ayub, Qasim, Bryndis Yngvadottir, Yuan Chen, Yali Xue, Min Hu, Sonja C. Vernes, Simon E. Fisher & Chris Tyler-Smith. 2013. FOXP2 targets show evidence of positive selection in European populations. *The American Journal of Human Genetics* 92, 696–706.
- Balari, Sergio & Guillermo Lorenzo. 2010. Communication. Where evolutionary linguistics went wrong. *Biological Theory* 5, 228–239.
- Balari, Sergio & Guillermo Lorenzo. 2012. Apología del villano. Richard Owen y el origen de Evo Devo. In Richard Owen, *Discurso sobre la naturaleza de las extremidades* [Sergio Balari & Guillermo Lorenzo (eds.)], 11–71. Oviedo: KRK.

- Balari, Sergio & Guillermo Lorenzo. 2013a. *Computational Phenotypes. Towards an Evolutionary Developmental Biolinguistics*. Oxford: Oxford University Press.
- Balari, Sergio & Guillermo Lorenzo. 2013b. Richard Owen and the mind/body problem. *Theoretical Biology Forum* 106, 131–146.
- Balari, Sergio & Guillermo Lorenzo. 2015a. Ahistorical homology and multiple realizability. *Psychological Philosophy* 28, 881–902.
- Balari, Sergio & Guillermo Lorenzo, 2015b. It is an organ, it is new, but it is not a new organ. Conceptualizing language from a homological perspective. *Frontiers on Ecology and Evolution* 3. doi:10.3389/fevo.2015.00058.
- Balari, Sergio & Guillermo Lorenzo. 2016. Evo-devo of language and cognition. In Laura Nuño de la Rosa & Gerd Müller (eds.), *Evolutionary Developmental Biology. A Reference Guide*. doi:"10.1007/978-3-319-33038-9_43-1".
- Bechtel, William. 2008. *Mental Mechanisms. Philosophical Perspectives on Cognitive Neuroscience*. New York: Psychology Press.
- Becker, Martin. 2016. On the identification of FOXP2 gene enhancers and their role in brain development. Nijmegen: Radboud University Nijmegen dissertation.
- Becker, Martin, Paolo Devanna, Simon E. Fisher & Sonia C. Vernes. 2015. A chromosomal rearrangement in a child with severe speech and language disorder separates FOXP2 from a functional enhancer. *Molecular Cytogenetics* 8, 69.
- Berwick, Robert C. & Noam Chomsky. 2011. The Biolinguistic Program: The current state of its development. In Anna Maria di Sciullo & Cedric Boeckx (eds.), *The Biolinguistic Enterprise. New Perspectives on the Evolution and Nature of the Human Language Faculty*, 19–41. Oxford: Oxford University Press.
- Berwick, Robert C. & Noam Chomsky. 2016. *Why Only Us. Language and Evolution*. Cambridge, MA: MIT Press.
- Bickle, John. 1998. *Psychoneural Reduction: The New Wave*. Cambridge, MA: The MIT Press.
- Bickle, John. 2003. *Philosophy of Neuroscience: A Ruthlessly Reductive Approach*. Dordrecht: Kluwer.
- Boeckx, Cedric. 2012. The I-language mosaic. In Cedric Boeckx, María de Carmen Horno-Chéliz & José Luis Mendivil-Giró (eds.), *Language, From a Biological Point of View*, 23–51. Newcastle upon Tyne: Cambridge Scholars Publishing.
- Boeckx, Cedric & Constantina Theofanopoulou. 2014. A multidimensional interdisciplinary framework for linguistics: The lexicon as a case study. *Journal of Cognitive Science* 14, 403–420.
- Bolhuis, Johan J., Ian Tattersall, Noam Chomsky & Robert C. Berwick. 2014. How could language have evolved? *PloS Biology* 12. doi:10.1371/journal.pbio.1001934.
- Bonkowsky, Joshua L. & Chi-Bin Chien. 2005. Molecular cloning and developmental expression of foxP2 in zebrafish. *Developmental Dynamics* 234, 740–746.
- Bonkowsky, Joshua L., Xu Wang, Esther Fujimoto, Ji Eun Lee, Chi-Bin Chien & Richard I. Dorsky. 2008. Domain-specific regulation of foxP2 CNS expression by *lef1*. *BCM Developmental Biology* 8, 103.
- Brentano, Franz C. 1874 [2009]. *Psychology from an Empirical Standpoint*. London: Routledge & Kean Paul.
- Buzsáki, György. 2006. *Rhythms of the Brain*. Oxford: Oxford University Press.

- Canguilhem, Georges. 1952. *Le connaissance de la vie*. Paris: Hachette.
- Castellucci, Gregg A., Matthew J. McGinley & David A. McCormick. 2013. Knockout of *Foxp2* disrupts vocal development in mice. *Scientific Reports* 6, 23305. doi:10.1038/srep23305
- Chabout, Jonathan, Abhra Sarkar, Sheel R. Patel, Taylor Radden, David B. Dunson, Simon E. Fisher & Erich D. Jarvis. 2016. A *Foxp2* mutation implicated in human speech deficits alters sequencing of ultrasonic vocalizations in adult male mice. *Frontiers in Behavioral Neuroscience* 10, 197. doi:10.3389/fnbeh.2016.00197.
- Chandrasekaran, Bharath, Han-Gyol Yi, Nathaniel J. Blanco, John E. McGeary & W. Todd Maddox. 2015. Enhanced procedural learning of speech sound categories in a genetic variant of FOXP2. *The Journal of Neuroscience* 35, 7808–7812.
- Chen, Qui, Tengzeng Zhu, Gareth Jones, Junpeng Zhang & Yi Sun. 2013. First knockdown gene expression in bat (*Hipposideros armiger*) brain mediated by lentivirus. *Molecular Biotechnology* 54, 564–571.
- Chiu, Yi-Chi, Ming-Yang Li, Yuan-Hsuan Liu, Jing-Ya Ding, Jenn-Yah Yu & Tsu-Wei Wang. 2014. *Foxp2* regulates neuronal differentiation and neuronal subtype specification. *Developmental Neurobiology* 74, 723–738.
- Chomsky, Noam. 1966. *Cartesian Linguistics. A Chapter in the History of Rationalist Thought*. New York: Harper & Row.
- Chomsky, Noam. 1968. *Language and Mind*. New York: Harcourt, Brace and World.
- Chomsky, Noam. 1993. *Language and Thought*. Wakefield, RI: Moyer Bell.
- Chomsky, Noam. 1995a. Language and nature. *Mind* 104, 1–61.
- Chomsky, Noam. 1995b. *The Minimalist Program*. Cambridge, MA: The MIT Press.
- Chomsky, Noam. 1997. Language and cognition. In David Martel Johnson & Christina E. Erneling, eds., *The Future of the Cognitive Revolution*, 15–31. New York: Oxford University Press.
- Chomsky, Noam. 2000. *New Horizons in the Study of Language and Mind*. Cambridge: Cambridge University Press.
- Chomsky, Noam. 2003. Reply to Lycan. In Louise M. Antony & Norbert Hornstein, eds., *Chomsky and His Critics*, 255–263. Malden, MA: Blackwell.
- Chomsky, Noam. 2013. Problems of projection. *Lingua* 113, 39–49.
- Chomsky, Noam. 2016. *What Kinds of Creatures Are We?* New York: Columbia University Press.
- Churchland, Paul M. 1989. *A Neurocomputational Perspective. The Nature of Mind and the Structure of Science*. Cambridge, MA: The MIT Press.
- Churchland, Patricia S. 1986. *Neurophilosophy. Toward a Unified Science of the Mind/Brain*. Cambridge, MA: The MIT Press.
- Churchland, Patricia S. & Terrence J. Sejnowski. 1992. *The Computational Brain*. Cambridge, MA: The MIT Press.
- Craver, Carl F. 2005. Beyond reduction: Mechanisms, multifield integration and the unity of neuroscience. *Studies in History and Philosophy of Biological and Biomedical Sciences* 36, 373–395.
- Craver, Carl F. 2007. *Explaining the Brain. Mechanisms and the Mosaic Unity of Neuroscience*. Oxford: Oxford University Press.
- Craver, Carl F. 2015. Levels. In Thomas Metzinger & Jennifer M. Windt, eds. *Open MIND*, 8(T). Frankfurt am Main: Open MIND Group. doi:10.15502/

9783958570498.

- Craver, Carl F. & Lindley Darden. 2013. *In Search of Mechanisms. Discoveries across the Life Sciences*. Chicago: The University of Chicago Press.
- Cummins, Robert. 1975. Functional analysis. *The Journal of Philosophy* 72, 741–765.
- Cummins, Robert. 1983. *The Nature of Psychological Explanation*. Cambridge, MA: The MIT Press.
- Cummins, Robert. 2002. Neo-teleology. In André Ariew, Robert Cummins & Mark Perlman, eds. *Functions. New Essays in the Philosophy of Psychology and Biology*, 157–172. Oxford: Oxford University Press.
- DasGupta, Shamik, Clara H. Ferreira & Gero Miesenböck. 2014. FoxP influences the speed and accuracy of a perceptual decision in *Drosophila*. *Science* 344, 901–904.
- Denisenko-Nehrbass, Natalia I., Eric D. Jarvis, Constance Scharff, Fernando Nottebohm & Claudio V. Mello. 2000. Site-specific retinoic acid production in the brain of adult songbirds. *Neuron* 27, 359–370.
- Denisenko-Nehrbass, Natalia I. & Claudio V. Mello. 2001. Molecular targets of disulfiram action on song maturation in zebra finches. *Molecular Brain Research* 87, 246–250.
- Dennett, Daniel C. 2017. *From Bacteria to Bach and Back. The Evolution of Minds*. London: Allen Lane.
- Devanna, Paolo, Jeroen Middlebeek & Sonja C. Vernes. 2014. FOXP2 drives neuronal differentiation by interacting with retinoic acid signaling pathways. *Frontiers in Cellular Neuroscience* 8, 305. doi:10.3389/fncel.2014.00305.
- Ding, Nai, Lucia Melloni, Hang Zhang, Xing Tian & David Poeppel. 2016. Cortical tracking of hierarchical linguistic structures in connected speech. *Nature Neuroscience* 19, 158–164.
- Eliasmith, Chris & Charles H. Anderson. 2003. *Neural Engineering: Computation, Representation, and Dynamics in Neurobiological Systems*. Cambridge, MA: The MIT Press.
- Enard, Wolfgang. 2011. FOXP2 and the role of cortico-basal ganglia circuits in speech and language evolution. *Current Opinion in Genetics and Development* 21, 415–424.
- Enard, Wolfgang. 2014. Mouse models of human evolution. *Current Opinion in Genetics and Development* 29, 75–80.
- Enard, Wolfgang, Sabine Gehre, Kurt Hammerschmidt, . . . , & Svante Pääbo. 2009. A humanized version of Foxp2 affects cortico-basal ganglia circuits in mice. *Cell* 137, 961–971.
- Enard, Wolfgang, Molly Przeworski, Simon E. Fisher, Cecilia S.L. Lai, Victor Wiebe, Takashi Kitano, Anthony Monaco & Svante Pääbo. 2002. Molecular evolution of FOXP2, a gene involved in speech and language. *Nature* 418, 868–872.
- Ereshfsky, Marc. 2012. Homology thinking. *Biology and Philosophy* 27, 382–400.
- Estruch, Sara B., Sarah A. Graham, Pelagia Deriziotis & Simon E. Fisher. 2016. The language-related transcription factor FOXP2 is post-translationally modified with small ubiquitin-like modifiers. *Scientific Reports* 6, 20911.
- Ferland, Russell J., Timothy Cherry, Patricia O. Preware, Edward E. Morrissey & Christopher A. Walsh. 2003. Characterization of Foxp2 and Foxp1 mRNA and protein in the developing and mature brain. *Journal of Comparative Neurology*

- 26, 266–279.
- Fisher, Simon E. & Constance Scharff. 2009. FOXP2 as a molecular window into speech and language. *Trends in Genetics* 26, 166–177.
- Fitch, W. Tecumseh. 2005. The evolution of language: A comparative review. *Biology and Philosophy* 20, 193–230.
- Fitch, W. Tecumseh. 2010. Deep Homology. In Ana M. Di Sciullo & Cedric Boeckx (eds.), *The Biolinguistic Enterprise: New Perspectives on the Evolution and Nature of the Human Language Faculty*, 135–166. Oxford: Oxford University Press.
- Fitch, W. Tecumseh, Noam Chomsky & Marc D. Hauser. 2005. The evolution of the language faculty: Clarifications and implications. *Cognition* 97, 179–210.
- Fodor, Jerry A. 1965. Explanations in psychology. In Max Black (ed.), *Philosophy in America*, 161–179. Ithaca, NY: Cornell University Press.
- Fodor, Jerry A. 1968. *Psychological Explanation: An Introduction to the Philosophy of Psychology*. New York: Random House.
- Fodor, Jerry A. 1974. Special sciences. *Synthese* 28, 77–115.
- Fodor, Jerry A. 1975. *The Language of Thought*. Cambridge, MA: Harvard University Press.
- Fodor, Jerry A. 1997. Special sciences: Still autonomous after all these years. *Noûs* 31 (Supplement: Philosophical Perspectives, 11, Mind, Causation, and World), 149–163.
- Fodor, Jerry A. & Massimo Piattelli-Palmarini. 2010. *What Darwin Got Wrong*. New York: Farrar, Straus & Giroux.
- Fontenot, Miles & Konopka, Genevieve. 2014. Molecular networks and the evolution of human cognitive specializations. *Current Opinion in Genetic and Development* 29, 52–59.
- Frixione, Marcello. 2001. Tractable competence. *Minds and Machines* 11, 379–397.
- Fujita-Jimbo, Eriko & Takashi Momoi. 2014. Specific expression of FOXP2 in cerebellum improves ultrasonic vocalization in heterozygous but not in homozygous FoxP2 (R552H) knock-in pups. *Neuroscience Letters* 566, 162–166.
- Gallistel, C. Randy & Adam Philip King. 2009. *Memory and the Computational Brain. Why Cognitive Science Will Transform Neuroscience*. Malden, MA: Wiley-Blackwell.
- Gehring, Walter J. & Ikeo Kazuko. 1999. Pax6: Mastering eye morphogenesis and eye evolution. *Trends in Genetics* 15, 371–377.
- Graham, Sarah & Simon E. Fisher. 2013. Decoding the genetics of speech and language. *Current Opinion in Neurobiology* 23, 43–51.
- Haesler, Sebastian, Kazuhiro Wada, A. Nshdejan, Edward E. Morrissey, Thierry Lints, Eric D. Jarvis and Constantine Scharff. 2004. FOXP2 expression in avian vocal learners and non-learners. *The Journal of Neuroscience* 24, 3164–3175.
- Haesler, Sebastian, Christelle Rochefort, Benjamin Georgi, Pawel Licznerki, Pavel Osten & Constance Scharff 2007. Incomplete and inaccurate vocal imitation after knockdown of FoxP2 in songbird basal ganglia nucleus Area X. *PLoS Biology* 5, e321. doi:10.1523/JNEUROSCI.4369-03.2004.
- Haugeland, John. 2002. Authentic intentionality. In Matthias Scheutz, ed. *Computationalism. New Directions*, 159–174. Cambridge, MA: The MIT Press.

- Hauser, Mark D., Noam Chomsky & W. Tecumseh Fitch. 2002. The faculty of language: What is it? Who has it? How did it evolve? *Science* 298, 1569–1579.
- Hauser, Mark D., Charles Yang, Robert C. Berwick, . . . , & Richard C. Lewontin. 2014. The mystery of language evolution. *Frontiers in Psychology* 5. doi:10.3389/fpsyg.2014.00401.
- Hempel, Carl & Paul Oppenheim. 1948. Studies in the logic of explanation. *Philosophy of Science* 15, 135–175.
- Hockett, Charles F. 1989. The origin of speech. *Scientific American* 6, 80–111.
- Itakura, Tatsuo, Abhishek Chandra, Zhi Yang, Xiao Dong Xue, Wataru Kimura, Keisuke Hikosaka, Keiji Inohaya, Akira Kudo, Tedayoshi Uezato & Naoyuki Miura. 2008. The medaka FoxP2, a homologue of human language gene FOXP2, has a diverged structure and function. *The Journal of Biochemistry* 143, 407–416.
- Jackendoff, Ray & Steven Pinker. 2005. The nature of the language faculty and its implications for the evolution of language (Reply to Fitch, Hauser and Chomsky). *Cognition* 97, 211–225.
- Johnson, Matthew B., Yuka Imamura Kawasaka, Chistopher E. Mason, Zeljika Krsnik, Giovanni Coppola, Darki Bodganovic, Daniel H. Geschwind, Shrikant M. Mane, Matthew W. State & Nenad Sestan. Functional and evolutionary insights into human brain development through global transcriptome analysis. *Neuron* 62, 494–509.
- Kaplan, David Michael & Carl F. Craver. 2011. The explanatory force of dynamical and mathematical models in neuroscience: A mechanistic perspective. *Philosophy of Science* 78, 601–627.
- Kim, Jaegwon. 2005. *Physicalism, or Something Near Enough*. Princeton, NJ: Princeton University Press.
- Kiya, Takeo, Y. Itoh & T. Kubo. 2008. Expression analysis of the FoxP homologue in the brain of the honeybee, *Apis mellifera*. *Insect Molecular Biology* 17, 53–60.
- Konopa Genevieve, Jamie M. Bomar, Kellen Winden, Giovanni Coppola, Zophonias O. Jonsson, Fuying Gao, Sophia Peng, Todd M. Preuss, James A. Wohlshlegel & Daniel H. Geschwind. 2009. Human-specific transcriptional regulation of CNS development genes by FOXP2. *Nature* 462, 213–217.
- Konopka, Genevieve, Tara Friedrich, Jeremy Davis-Turak, Kellen Winden, Michael C. Oldham, Fuying Gao, Leslie Chen, Guang-Zhong Wang, Rui Luo, Todd M. Preuss & Daniel Geschwind. 2012. Human-specific transcriptional networks in the brain. *Neuron* 75, 601–617.
- Konopka, Genevieve & Geschwind, Daniel H. 2010. Human brain evolution: Harnessing the genomics (r)evolution to link genes, cognition, and behavior. *Neuron* 68, 231–244.
- Kopell, Nancy J., Howard J. Gritton, Miles A. Whittington & Mark A. Kramer. 2014. Beyond the connectome: The Dynome. *Neuron* 83, 1319–1328.
- Lai, Cecilia S., Simon E. Fisher, Jane A. Hurst, Faraneh Vargha-Khadem & Anthony P. Monaco. 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413, 519–253.
- Lai, Cecilia S.L., Dianne Gerrelli, Anthony P. Monaco, Simon E. Fisher & Andrew J. Copp. 2003. FOXP2 expression during brain development coincides with adult sites of pathology in a severe speech and language disorder. *Brain* 126,

- 2455–2462.
- Lawton, Kristy J., Taryn L. Wassmer & David L. Deitcher. 2014. Conserved role of *Drosophila melanogaster* FoxP in motor coordination and courtship song. *Behavioral Brain Research* 268, 213–221.
- Lenneberg, Eric H. 1967. *Biological Foundations of Language*. New York: John Wiley & Sons.
- Lenneberg, Eric H. 1969. On explaining language. *Science* 164, 635–643.
- Lewis, Ashley G. & Marcel Bastiaansen. 2015. A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex* 68, 155–168.
- Lewis, Ashley G., Lin Wang & Marcel Bastiaansen. 2015. Fast oscillatory dynamics during language comprehension: Unification versus maintenance and prediction?. *Brain & Language* 148, 51–63.
- Li, Gang, Jinhong Wang, Stephen J. Rossiter, Gareth Jones & Shuyi Zhang. 2007. Accelerated *FoxP2* evolution in echolocating bats. *PLoS ONE* 2, e900. doi:10.1371/journal.pone.0000900.
- Liégeois, Frédérique, Torsten Badelweg, alan Connelly, David G. Gadian, Mishkin, Mortimer & Faraneh Varga-Khadem. 2003. Language fMRI abnormalities associated with *FOXP2* gene mutation. *Nature Neuroscience* 6, 1230–1237.
- Love, Alan C. 2007. Functional homology and homology of function: Biological concepts and philosophical consequences. *Biology & Philosophy* 22, 691–708.
- Lycan, William G. 2003. Chomsky on the Mind-Body Problem. In Louise M. Antony & Norbert Hornstein, eds., *Chomsky and His Critics*, 11–28. Malden, MA: Blackwell.
- Machamer, Peter, Lindley Darden & Carl F. Craver. 2000. Thinking about mechanisms. *Philosophy of Science* 67, 1–25.
- Marr, David. 1982. *Vision*. San Francisco: W. H. Freeman.
- Mayr, Ernst. 1960. The emergence of evolutionary novelties. In Sol Tax (ed.), *Evolution After Darwin. The University of Chicago Centennial, Vol.1: The Evolution of Life. Its Origin, Evolution and Future*, 349–380. Chicago, IL: The University of Chicago Press.
- Medvedeva, Vera. 2015. *Characterization of Foxp2 functions in the mouse cortex*. Paris: Université Pierre et Marie Curie dissertation.
- Mendoza Ezequiel, Julien Colomb, Jürgen Rybak, Hans-J. Pflüger, Troy Zars, Constance Scharff & Björn Brembs. 2014. *Drosophila* FoxP mutants are deficient in operant self-learning. *PLoS One* 9, e100648. doi:10.1371/journal.pone.0100648.
- Millikan, Ruth G. 1984. *Language, Thought, and Other Biological Categories. New Foundations for Realism*. Cambridge, MA: The MIT Press.
- Murphy, Elliot. 2015. The brain dynamics of linguistic computation. *Frontiers in Psychology* 6: 1515. doi:10.3389/fpsyg.2015.01515.
- Murphy, Elliot. 2016. The human oscillome and its explanatory potential. *Biolinguistics* 10, 6–20.
- Müller, Gerd B. & Günter P. Wagner. 1991. Novelty in evolution: Restructuring the concept. *Annual Review of Ecology and Systematics* 22, 229–256.
- Müller, Gerd B. & Günter P. Wagner. 2003. Innovation. In Brian K. Hall & Wendy M. Olson (eds.), *Keywords and Concepts in Evolutionary Developmental Biology*,

- 218–227. Cambridge, MA: Harvard University Press.
- Newbury, Dianne F., Simon E. Fisher & Anthony Monaco. 2010. Recent advances in the genetics of language impairment. *Genome Medicine* 2, 6. doi:10.1186/gm127.
- Newbury, Dianne F. & Anthony Monaco. 2010. Genetic advances in the study of speech and language disorders. *Neuron* 68, 309–320.
- Nitecki, Matthew H. (ed.). 2016. *Evolutionary Innovations*. Chicago, IL, and London: The University of Chicago Press.
- Oppenheim, Paul & Hilary Putnam. 1958. Unity of science as a working hypothesis. In Herbert Feigl, Michael Scriven & Grover Maxwell, eds. *Concepts, Theories, and the Mind-Body Problem*. *Minnesota Studies in the Philosophy of Science II*, 3–36. Minneapolis: University of Minnesota Press.
- Owen, Richard. 1843. *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals*. London: Longman, Brown, Green and Longmans.
- Owen, Richard. 1849. *On the Nature on Limbs. A Discourse*. London: John Van Voorst.
- Pfenning, Andreas R., Erina Hara, Osceola Whitney, ..., & Eric D. Jarvis. 2014. Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science* 346, doi:10.1126/science.1256846.
- Phillmore, Leslie S., Heather L. MacGillivray, K. Ryan Wilson & Stephanie Martin. 2014. Effects of sex and seasonality on the song control system and FoxP2 protein expression in black-capped chickadees (*Poecile atricapillus*). *Developmental Neurobiology* 75, 203–216.
- Piccinini, Gualtiero. 2007. Computing mechanisms. *Philosophy of Science* 74, 501–526.
- Piccinini, Gualtiero. 2015. *Physical Computation. A Mechanistic Account*. Oxford: Oxford University Press.
- Piccinini, Gualtiero & Sonya Bahar. 2013. Neural computation and the computational theory of cognition. *Cognitive Science* 34, 453–488.
- Piccinini, Gualtiero & Carl F. Craver. 2011. Integrating psychology and neuroscience: functional analyses as mechanism sketches. *Synthese* 183, 283–311.
- Piccinini, Gualtiero & Oron Shagrir. 2014. Foundations of computational neuroscience. *Current Opinion in Neurobiology* 25, 25–30.
- Pinker, Steven & Ray Jackendoff. 2005. The faculty of language: What's special about it. *Cognition* 95, 201–236.
- Poeppl, David. 2012. The maps problem and the mapping problem: Two challenges for a cognitive neuroscience of speech and language. *Cognitive Neuropsychology* 29, 34–55.
- Poeppl, David & David Embick. 2005. Defining the relation between linguistics and neuroscience. In Anne Cutler, ed., *Twenty-First Century Psycholinguistics: Four Cornerstones*, 103–118. Mahwah, NJ: Lawrence Erlbaum.

- Poland, Jeffrey. 2003. Chomsky's challenge to physicalism. In Louise M. Antony & Norbert Hornstein, eds., *Chomsky and His Critics*, 29–48. Malden, MA: Blackwell.
- Polger, Thomas W. 2004. *Natural Minds*. Cambridge, MA: The MIT Press.
- Polger, Thomas W. & Lawrence A. Shapiro. 2016. *The Multiple Realization Book*. Oxford: Oxford University Press.
- Preuss, Todd M. 2012. Human brain evolution: From gene discovery to phenotype discovery. *Proceedings of the National Academy of Sciences U.S.A.* 109, 10709–10716.
- Putnam, Hilary. 1975. The nature of mental states. In *Mind, Language and Reality: Philosophical Papers, Vol 2*, 429–440. Cambridge: Cambridge University Press.
- Reimers-Kipping, S. W. Hevers, S. Pääbo & W Enard. 2011. Humanized Foxp2 specifically affects cortico-basal ganglia circuits. *Neuroscience* 175, 75–84.
- Richards, Robert J. 2002. *The Romantic Conception of Life. Science and Philosophy in the Age of Goethe*. Chicago: The University of Chicago Press.
- Richards, Robert J. 2005. Darwin's metaphysics of mind. In V. Höhle & Ch. Illies, eds., *Darwinism and Philosophy*, 166–180. Notre Dame, IN: University of Notre Dame Press.
- Rieke, Fred, David Warland, Rob de Ruyter van Steveninck & William Bialek. 1997. *Spikes. Exploring the Neural Code*. Cambridge, MA: The MIT Press.
- Rodenas-Cuadrado, Pedro, Jose Ho & Sonja C. Vernes. 2014. Shining a light on CNTNAP2: Complex functions to complex disorders. *European Journal of Human Genetics* 22, 171–178.
- Roll, Patrice, Sonja C. Vernes, Nadine Bruneau, Jennifer Cillario, Magali Ponsole-Lenfnt, Annick Massacrier, Gabrielle Rudolf, Manal Khalife, Edouard Hirsh, Simon E. Fisher & Pierre Szepetowski. 2010. Molecular networks implicated in speech-related disorders: FOXP2 regulates the SRPX2/uPAR complex. *Human Molecular Genetics* 19, 4848–4860.
- Roeske, Christina. 2010. The role of retinoid signaling in the song control system of the zebra finch: From molecules to behavior. The neurobiological basis of song learning in songbirds. Berlin: Freie Universität dissertation.
- Roeske, Tina C., Constance Scharff, Christopher R. Olson, Arpik Nshdejan & Claudio V. Mello. 2014. Long-distance retinoic signaling in the zebra finch brain. *PLoS ONE* 9, e111722. doi:10.1371/journal.pone.0111722.
- Scharff, Constance & Jana Petri. 2011. Evo-devo, Deep homology and FoxP2: Implications for the evolution of speech and language. *Philosophical Transactions of the Royal Society B* 266, 2124–2140.
- Schneider, Gerald E. 2014. *Brain Structure and Its Origins in Development and in Evolution of Behavior and the Mind*. Cambridge, MA: The MIT Press.
- Schreiweis, Christiane, Ulrich Bornschein, Eric Burgière, . . . , & Ann. M. Graybel. 2014. Humanized Foxp2 accelerates learning by enhancing transitions from declarative to procedural performance. *Proceedings of the National Academy of Sciences U.S.A.* 111, 14253–14258.
- Searle, John R. 1992. *The Rediscovery of Mind*. Cambridge, MA: MIT Press.
- Seung, Sebastian. 2012. *Connectome: How the Brain's Wiring Makes Us Who We Are*. London: Penguin.

- Shagrir, Oron. 2010. Marr on computational-level theories. *Philosophy of Science* 77, 477–500.
- Shah, Rina, Olga Medina-Martínez, Li-Fang Chu, Rodney C. Samaco & Milan Jamrich. 2006. Expression of *FoxP2* during zebrafish development and in the adult brain. *International Journal of Developmental Biology* 50, 435–438.
- Shu, Weiguo, Julie Y. Cho, Yuhui Jiang, . . . , & Joseph D. Buxbaum. 2007. Altered ultrasonic vocalization in mice with a disruption in the *Foxp2* gene. *Proceedings of the National Academy of Sciences U.S.A.* 102, 9643–9648.
- Shubin, Neil, Cliff Tabin & Sean Carroll. 1997. Fossils, genes and the evolution of animal limbs. *Nature* 388, 639–648.
- Shubin, Neil, Cliff Tabin & Sean Carroll. 2009. Deep homology and the origins of evolutionary novelty. *Nature* 457, 818–823.
- Smith, Brian Cantwell. 2002. The foundations of computing. In Matthias Scheutz, ed., *Computationalism. New Directions*, 23–58. Cambridge, MA: The MIT Press.
- Smolensky, Paul & Géraldine Legendre. 2006. Harmony optimization and the computational architecture of the mind/brain. In Paul Smolensky & Géraldine Legendre, eds. *The Harmonic Mind: From Neural Computation to Optimality-Theoretic Grammar. Volume 1: Cognitive Architecture*, 3–61. Cambridge, MA: The MIT Press.
- Stich, Stephen. 1983. *From Folk Psychology to Cognitive Science. The Case Against Belief*. Cambridge, MA: The MIT Press.
- Teramitsu, Ikuko, Lili C. Kudo, Sarah E. London, Daniel H. Geschwind & Stephanie A. White. 2004. Parallel FoxP1 and FoxP2 expression in songbird and human brain predicts functional interaction. *Journal of Neuroscience* 24, 3152–3163.
- Torres-Ruiz, Raul, Antonio Benítez-Burraco, Marta Martinez-Lage, Sandra Rodríguez-Perales & Paloma García-Bellido. 2016. Functional genetic characterization by CRISPR-Cas9 of two enhancers of FOPX2 in a child with speech and language impairment. *bioRxiv*. doi:10.1101/064196.
- Usui, Noriyoshi, Marissa Co, Matthew Harper, Michael A. Rieger, Joseph D. Dougherty & Genevieve Konopka. 2017. Sumoylation of FOXP2 regulates motor function and vocal communication through Purkinje cell development. *Biological Psychiatry* 81, 220–230.
- van Gelder, Tim. 1995. What might cognition be, if not computation?. *The Journal of Philosophy* 92, 345–381.
- van Gelder, Tim. 1998. The dynamical hypothesis in cognitive science. *Behavioral and Brain Sciences* 21, 615–665.
- van Rhijn, Jon-Ruber & Sonja C. Vernes. 2015. Retinoic Acid signaling: A new piece in the spoken language puzzle. *Frontiers in Psychology* 6, 1816. doi:10.3389/fpsyg.2015.01816.
- van Rooij, Iris. 2008. The Tractable Cognition thesis. *Cognitive Science* 32, 939–984.
- Vernes, Sonja C. 2017. What bats have to say about speech and language. *Psychonomic Bulletin and Review* 24, 111–117.
- Vernes, Sonja C. & Simon E. Fisher. 2009. Unravelling neurogenetic networks implicated in developmental language disorders. *Biochemistry Society Transactions* 37, 1263–1269.
- Vernes, Sonja C., Peter L. Oliver, Elizabeth Spiteri, . . . , & Simon E. Fisher. 2011. *Foxp2* regulates gene networks implicated in neurite outgrowth in the devel-

- oping brain. *PLoS Genetics* 7, e1002145. doi:10.1371/journal.pgen.1002145.
- Wagner, Andreas. 2011. *The Origins of Evolutionary Innovations*. Princeton, NJ, & Oxford: Princeton University Press.
- Wagner, Günter P. 1989. The biological homology concept. *Annual Review of Ecology and Systematics* 20, 51–59.
- Wagner, Günter P. 2014. *Homology, Genes, and Evolutionary Innovation*. Princeton, NJ: Princeton University Press.
- Wagner, Günter P. 2015. What is ‘homology thinking’ and what is it for? *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 326, 3–8.
- Webb, D.M. & J. Zhang. 2005. *FoxP2* in song-learning birds and vocal-learning mammals. *Journal of Heredity* 96, 212–216.
- Webb, Helen Susannah. 2015. *Binding studies of the FOXP2 forkhead domain and its cognate DNA sequences*. Johannesburg: University of Witwatersrand dissertation.
- Wheeler, Michael. 2005. *Reconstructing the Cognitive World. The Next Step*. Cambridge, MA: MIT Press.
- White, Stephanie A., Simon E. Fisher, Daniel H. Geschwind, Constance Scharff & Timothy E. Holy. 2006. Signing mice, songbirds, and more: Models for FOXP2 function and dysfunction in human speech and language. *Journal of Neuroscience* 26, 10376–10379.
- Wouters, Arno G. 2003. Four notions of biological function. *Studies in History and Philosophy of Biological and Biomedical Sciences* 34, 633–668.

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